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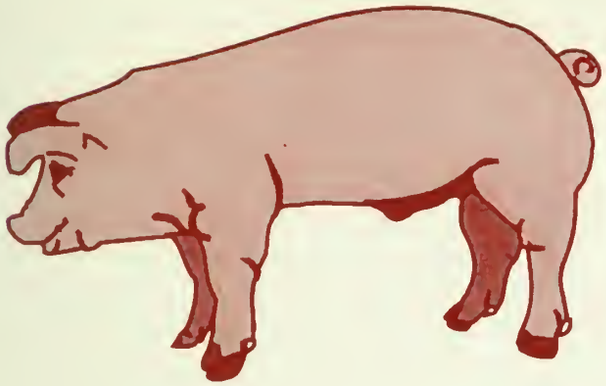

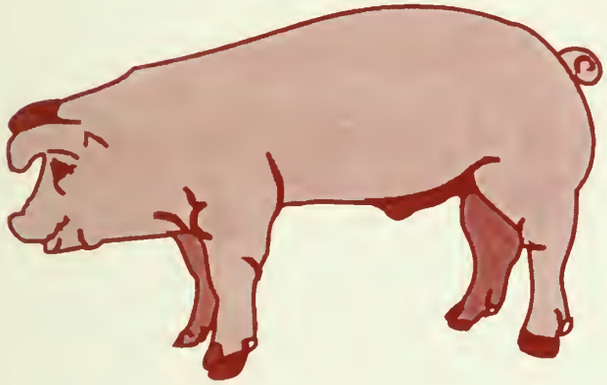

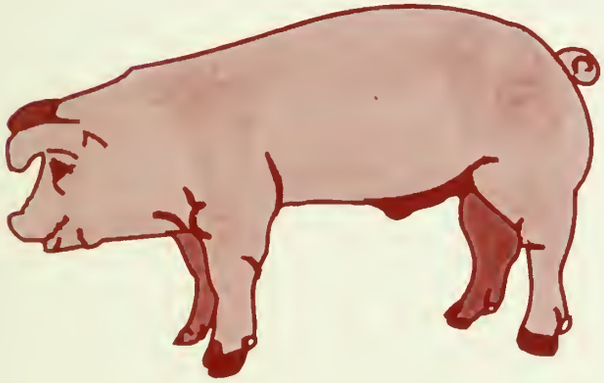

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PORK INDUSTRY CONFERENCE

November 9-10, 1995
College of Agricultural, Consumer and Environmental Sciences
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University of Illinois
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"Management for Quality Pork Production"

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University of Illinois at Urbana-Champaign

University of Illinois
PORK INDUSTRY CONFERENCE
November 9-10, 1995
University Inn, Champaign, Illinois

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THE PORK QUALITY CHALLENGE

F. K. McKeith, M. Ellis, T. R. Carr

Animal agriculture is continually facing challenges to maintain/increase their share of the consumer's meat dollar. Livestock production has changed to reflect consumer demand for meat over the past several decades (Table 1). Reviewing the per capita consumption of meat for the past 20 years suggests several key points: 1) total meat consumption on a boneless equivalent basis is approximately 190 lbs. per person per year or .5 lb per person per day, 2) consumption of beef, veal, and lamb has decreased during the last 20 years, 3) poultry consumption has increased dramatically in the past 20 years, and 4) pork consumption has been relatively static.

A variety of factors influence consumption of meat including: 1) price, 2) perceived value, 3) diet/ health considerations 4) convenience, and/or 5) quality/palatability. Many of these traits are related to each other. One of the factors that has received a great deal of attention during the past several years is quality.

At the present time, quality is perceived differently by different groups between the producer and consumer. The National Pork Quality Audit identified up to twenty-one different potential market interfaces between producers and consumers. The perception and definition of quality differs among people within a group as well as between groups. Quality may be defined as the degree or grade of excellence.

The Pork Quality Audit (1994) characterized quality defects at slaughter, fabrication, and processing components of the meat industry. An economic evaluation of the results suggested that more than $10.08 and $2.32/head is lost due to quality defects at slaughter and processing, respectively. This value represents approximately 10% of the value of a pig (Table 2 and 3).

Carcass fatness is the largest economic cost associated with nonconformities in the slaughter and fabrication industry. It accounted for more than 50% of the loss in value for this segment of the industry. Variation in weight, carcass trimming condemnations, and color/water holding capacity problems all resulted in significant economic losses ($.71 to $1.23/head). Trim specifications (amount of skin and/or fat) had the largest economic impact ($1.02) for processors. Pale, soft, exudative muscle (PSE) was associated with a loss of $.44 per head for processors. It is important to recognize that these values are estimated on the economic loss of these two market interfaces and does not address economic losses at subsequent points in the pork chain. Estimation of the economic consequence of meat quality or appearance traits (seam fat, PSE, intramuscular fat, etc.) at the consumer level is very difficult.

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Carcass composition is the area of greatest economic consequence identified in the Pork Quality Audit (1994). A variety of approaches have been used to improve carcass composition including genetics, nutrition, management, and growth modifiers. Several of the papers presented in this conference will address the issues of reducing carcass fatness. There appears to be limited, if any, relationship between carcass composition and palatability of pork (Rhodes, 1970; Wood et al., 1981; Wood et al., 1986; and DeVvol et al., 1988).

The relationship between intramuscular fat (marbling) and palatability has been identified as a potential means of predicting palatability of pork. DeVol et al. (1988) and Hodgson et al. (1991) reported a significant relationship between intramuscular fat and tenderness in pork, however, the correlations were low (r= -.14 and -.36, respectively, for Warner Bratzler Shear Force). The relationship between intramuscular fat and juiciness differed a great deal between the two studies. Hodgson et al. (1991) reported a correlation of .71 and DeVol et al. (1988) reported a correlation of .23.

The PSE condition occurs when the muscle from a pork carcass is pale in color, has a soft texture, and is exudative or watery. A rapid decline in pH, due to accelerated anaerobic glycolysis, combined with high carcass temperature results in the denaturation of approximately 20% of the sarcoplasmic and myofibrillar proteins (Honikel and Kim, 1986). High moisture loss is caused by the denaturation of myosin prior to the onset of rigor mortis. The fraction of myosin denatured will increase with the rate of pH decline. The maximum pH drop is dependent upon the chilling rate and related conditions. The percentage of denatured protein increases at a lower ultimate pH. In general, with an increase in the rate of chilling, there is a decrease in the percentage of denatured proteins because anaerobic glycolysis is reduced and pH decline is slowed (Offer, 1991). Low 45-minute muscle pH and slow heat dissipation from the muscle has been associated with PSE pork (Didley et al., 1970).

In a survey of 14 packing plants, Kauffman et al. (1992) reported that approximately 26% of pork produced was undesirable (16% PSE and 10% dark, firm, and dry). Additionally, there was great variation in the muscle quality of pork products between the different packing plants which was attributed to the variation in handling practices that influenced the amount of stress placed on the animals immediately prior to slaughter (Kauffman et al., 1992). The Pork Quality Audit reported a lower incidence for both PSE and DFD. The difference in the incidence of the problem may be attributed to sample size, environmental conditions at the time of sampling or differing criteria to characterize the carcasses into groups.

Studies have been conducted to evaluate procedures, both antemortem and postmortem, to reduce the incidence of PSE meat (Borchert and Briskey, 1964; Kastenschmidt et al., 1964; Honkavaara, 1989a: Eikelenboom et al., 1991; Offer, 1991). It is believed that the most effective way to reduce the incidence of poor quality pork, other than through genetics, is to improve preslaughter management and handling. Reduced stress during loading, transport and handling, improved environmental conditions, and shorter travel times are some of the methods which could reduce the problem of PSE pork. The use of improved preslaughter handling has proven to be an effective means of reducing PSE and unnecessary death loss

(Sybesma, 1980; and Murray, 1982).

Handling of the pork carcass may also influence meat quality. Scalding and dehairing of the carcass to remove hair increases carcass temperature which accelerates glycolysis (Honkavaara, 1989b). These procedures increase the incidence of PSE because the rates of glycolysis and glycogenolysis are increased. A reduction in the pH, via anaerobic glycolysis combined with high carcass temperature, results in rapid pH declines and an increase in the incidence of PSE (Honkavaara, 1989b).

Probably the most economically important aspect of PSE pork is the inability to the meat to bind water. During transit, PSE hams lose three times more moisture than do normal hams and seven times more moisture than do dark, firm, and dry (DFD) hams (Kauffman et al., 1978). In addition, moisture losses during curing, smoking, and chilling are greater in PSE hams than in normal hams and three times greater than in DFD hams (Kauffman et al., 1978). Hams with severe PSE have a water holding capacity (WHC) of 33% below that of normal hams, and PSE shoulders have WHC values of 11% below those of normal pork. Honkavaara (1990) found that the addition of phosphate to pork with severe PSE did not improve water holding capacity and that 1.5% more pork trimmings are needed for PSE pork compared to normal pork to absorb the same amount of added water during processing (Honkavaara, 1990). Moisture loss is of great economic significance to pork processors and meat retailers due to reduced processed and storage yields.

The inability of PSE meat to bind water leads to many other problems. Reduced tenderness, often due to increased cooking losses, may be observed with PSE muscle (van der Wal et al., 1989). Consumer panel scores for acceptability were lower for pale colored chops, and trained panel scores for tenderness were less desirable for PSE chops compared to normal pork chops (Topel et al., 1976). Boles et al. (1991) observed similar results when comparing sensory characteristics of chops from animals of three different halothane genotypes. Chops from animals which carried the halothane gene were less tender than chops from animals that did not carry the halothane gene, while chops from halothane positive animals had decreased tenderness compared to chops from halothane-carrier animals (Boles et al., 1991).

Death loss and the loss of portions of carcasses are associated with economic losses in excess of $2/head. Swine death loss during transport is a producer-related problem that can be avoided. Studies have shown an increase in the mortality rate of hogs during transport when the animals were fed the same day (Eikelenboom, 1988; Guise and Warriss, 1989). Guise and Warriss (1989) found that pigs transported under cold conditions had a slightly lower ultimate pH than those transported at more moderate temperatures. Additionally, the length of transport plays a role in swine mortality. Honkavaara (1989a) concluded that mortality rates are the lowest for 10-25 min transport and the highest when hogs are transported for 45-80 min. In the U.S., approximately 80% of hogs are shipped more than 50 miles prior to slaughter. With an increase in the number of long transports, it is necessary for swine producers to implement management practices that will minimize death losses.

Loading density during transport has an effect on death loss as well as the incidence of injury

and PSE muscle. It is important to allow enough room in the truck or trailer for each individual pig, particularly in hot, humid weather. If pigs are not allowed enough space, there is a greater chance for injury. Overcrowding also contributes to stress-related meat quality problems in swine, particularly during periods of hot weather. The Meat and Livestock Commission in the United Kingdom has recommended a space allowance of 0.4-0.5m^2 for pigs being transported to slaughter (Guise and Warriss, 1989).

Economic losses are also associated with slaughter industry. The major concerns about pork quality that are related to methods/conditions of stunning are PSE, ecchymosis (blood splash) and broken bones. All stunning techniques pose some type of quality concern, so operator practices become a critical component in controlling quality defects.

Pale, soft, and exudative pork becomes a problem when hogs are stressed immediately before stunning. Struggling at death will increase lactic acid production and will accelerate the decline in muscle pH (Carr, 1985). All stunning methods cause some stress in animals, however, the magnitude of the stress depends on the individual stunning technique (Carr, 1985). Overstreet et al. (1975) compared the rate of muscle glycolysis in pigs stunned using 90 volts vs. 120 volts of electricity, carbon dioxide, and the captive bolt pistol and recommended that stunning with the captive bolt pistol should not be used because of increased anaerobic glycolysis in pork muscle. Results of the study suggested minimal differences in muscle quality between electrical stunning and the use of carbon dioxide (Overstreet et al., 1975). Electrical stunning is the most widely used technique for stunning in the U.S.

Broken bones are directly related to electrical stunning. The scapula and/or femur, for example, may fracture during stunning while pigs feet are in contact with the floor. Additionally, when pigs are stunned head to back at excessive voltage, the vertebrae may fracture (Tarrant, 1993). Costly trimming is required in the area surrounding broken bones to remove damaged tissue and bone chips. Bone breakage occurs only during electrical stunning and is seen as a major disadvantage to its use (Tarrant, 1993).

Another quality problem related to improper stunning is blood splash. Blood splashing probably results from blood-vessel aneurysms caused by severe muscle contractions while systolic blood pressure is high (Gregory, 1987). Electrical stunning as well as captive-bolt pistol stunning are the primary contributors to blood splashing. When using electrical stunning, previous work has recommended the use of higher voltage (240v) as a means to reduce the incidence/severity of blood splash (Cooper et al., 1980). Probably the most practical method of reducing the incidence of blood splashing is to reduce the time between stunning and bleeding. Tarrant (1993) recommended sticking no later than 10 seconds after stunning which is well before the kicking phase that results in severe muscle contractions. Additionally, Carr (1985) recommended that the time between stunning and bleeding should not exceed 60 seconds as the incidence of blood splash increases after this time period.

Scalding and dehairing is the most common system used by the major U.S. Packers to remove hog hair. Carcasses are scalded at high temperatures (140°F) and then run through a dehairing machine. After washing, to remove loose hair, the carcass is singed to remove the remaining

hair. Compared to skinning, scalding/dehairing is a more practical and efficient means of removing the hair from pigs at the high chain-speeds currently being used in the U.S.

The primary disadvantage to using the scalding/dehairing process is quality problems which are influenced by accelerated postmortem glycolysis (Carr, 1985) Postmortem anaerobic glycolysis is accelerated at high carcass temperatures, and excessive lactic acid is produced. The resultant low ultimate pH (Troeger and Woltersdorf, 1987; Honkavaar, 1989b), as well as the reduced pH at high body temperature, results in protein denaturation and produces the characteristic PSE muscle condition. Previous studies have suggested that meat from skinned carcasses compared to scaled carcasses has improved muscle color and water holding capacity (Voogd, 1983; Troeger and Woltersdorf, 1987).

Rate of carcass chilling influences the quality and shelf-life of pork with regards to future uses as both fresh and processed meat. Quality characteristics such as water holding capacity, tenderness, and microbial load can be affected by type and form of chilling. Chilling rate (Borchert and Briskey, 1964; Crenwelge et al., 1984a, b; Gigiel et al., 1989; Ortner, 1989; Feldhusen and Kuhne, 1992; Feldhusen et al., 1992) and electrical stimulation (Crenwelge et al., 1984a,b; Gigiel and James, 1984) have been evaluated in efforts to improve pork quality characteristics.

Electrical stimulation is commonly used in the beef industry to accelerate postmortem metabolism, to brighten muscle color, to improve quality grade, and improve tenderness (Cross, 1979). Electrical stimulation has had mixed effects, in research studies, on the quality parameters of pork. Gigiel and James (1984) reported improved tenderness in chops from electrically stimulated pork carcasses compared to chops from non-stimulated carcasses. On the other hand, Crenwelge et al. (1984a, b) observed increased occurrence of pale muscle color, muscle separation, and muscle softness in electrically stimulated pork carcasses. Tenderness was not improved by electrical stimulation in the Crenwelge et al. (1984 a, b) studies.

Rapid chilling is a procedure used in the pork industry to reduce the incidence of PSE pork and to improve pork quality characteristics. Rapid chilling immediately after slaughter slows the rate of muscle glycolysis, resulting in a higher ultimate muscle pH and a reduced incidence of PSE pork (Carr, 1985). Borchert and Briskey (1964) observed reduced incidences of PSE pork when cuts were immersed in liquid nitrogen. Crenwelge et al. (1984a, b) observed improved pork color and firmness and decreased muscle separation when carcasses were rapidly chilled (3 h at -29°F then 21 h at 36°F).

Overall, there are a variety of quality issues that can be addressed by the production and slaughter segments of the industry that can have significant economic benefit to the entire pork industry.

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TABLE 1

Per Capita Consumption of Red Meat, Poultry and Fish, Boneless Equivalent, 1979-1993

Year	Beef	Veal	Pork	Lamb	Chicken	Turkey	Fish	Total Red Meat, Poultry and Fish
				Pounds				
1970	79.6	2.0	48.0	2.1	27.4	6.4	11.7	177.3
1971	79.0	1.9	52.6	2.1	27.4	6.6	11.5	181.0
1972	80.3	1.6	47.8	2.2	28.3	7.1	12.5	179.7
1973	75.8	1.2	43.0	1.7	27.1	6.6	12.7	168.2
1974	80.6	1.6	46.7	1.5	27.0	6.8	12.1	176.3
1975	83.0	2.8	38.7	1.3	26.4	6.5	12.1	170.9
1976	88.8	2.7	40.3	1.2	28.5	7.0	12.9	181.4
1977	86.3	2.6	42.3	1.1	29.0	6.9	12.6	180.9
1978	82.2	2.0	42.3	1.0	30.4	6.9	13.4	178.2
1979	73.5	1.4	48.6	1.0	32.7	7.3	13.0	177.4
1980	72.1	1.3	52.1	1.0	32.5	8.1	12.4	179.4
1981	72.8	1.3	49.9	1.0	33.5	8.3	12.6	179.5
1982	72.5	1.4	44.9	1.1	33.7	8.3	12.4	174.2
1983	74.1	1.4	47.4	1.1	33.9	8.7	13.3	179.8
1984	73.8	1.5	47.2	1.1	35.0	8.7	14.1	181.5
1985	74.6	1.5	47.7	1.1	36.1	9.1	15.0	185.1
1986	74.4	1.6	45.2	1.0	37.0	10.2	15.4	184.7
1987	69.5	1.3	45.6	1.0	39.1	11.6	16.1	184.2
1988	68.6	1.1	48.8	1.0	39.3	12.4	15.1	186.3
1989	65.4	1.0	48.4	1.1	40.5	13.1	15.6	185.1
1990	63.9	0.9	46.4	1.1	41.5	13.8	15.0	182.7
1991	63.5	0.8	47.0	1.1	43.5	14.2	14.9	184.0
1992	62.8	0.8	49.5	1.0	45.9	14.2	14.8	189.0
1993	61.4	0.8	48.8	1.0	47.0	14.1	14.9	188.0

AMI(1994)

TABLE 2
PORK CHAIN QUALITY AUDIT ESTIMATE OF ECONOMIC LOSS ASSOCIATED WITH NONCONFORMITIES IN CARCASS QUALITY

Trait/Defect	Cost/Head
Condemnation	$1.00
Deviations ideal live weight	.88
Trimming for skin problems, bruises, abscesses, arthritis and/or broken bones	1.23
Two-toned muscle color and DFD	.27
Ecchymosis	.49
Pale, soft, watery muscle	.34
Miscut carcasses and cuts	.22
Excessive backfat	2.85
Excess external fat - ham	1.32
Excess external fat - Boston butt	.72
Excessive seam fat	.63
Thin bellies	.13
Total cost	**$10.08**

Cannon et al. (1995)

TABLE 3
PORK C HAIN AUDIT ESTIMATE OF ECONOMIC LOSS ASSOCIATED WITH PROCESSING NONCONFORMITIES

HAM	Cost/Hog
Foreign objects	$0.05
Injection sites/abscesses	0.03
Bruises	0.08
Trim specification	0.57
Pale, soft, exudative	0.25
Total Ham Costs	**0.98**
BACON	
Abscesses	0.01
Skin problems	0.05
Trim specification	0.45
Pale, soft, exudative	0.09
Thin bellies	0.25
Total Bacon Costs	**0.85**
SAUSAGE	
Foreign objects	0.02
Abscesses	0.02
Bruises/blood clots	0.12
Pale, soft, exudative	0.10
Total Sausage Costs	**0.26**
Quality Control/Production Costs	**.23**
TOTAL COST	**$2.32**

Cannon et al. (1995)

Genetics and Meat Quality

Dr. Mike Ellis

Introduction

The issue of pig meat quality is a relatively recent but increasingly important phenomenon in the swine industry. Our understanding of factors influencing quality aspects is also relatively recent, although the speed of development of this understanding has been very dramatic. One of the major limitations to progress in this area has been the lack of consensus between and within the various sectors of the industry on appropriate definitions of pig-meat quality.

Meat quality has many components which vary in their relative economic importance between and within sectors and, in addition, communication within the industry has not always been good. This situation is, however, changing rapidly and there are now much closer ties between the various industry sectors which has resulted in a clearer understanding of the extent of quality problems.

The consumer is the ultimate arbiter of meat quality and attempts to identify important quality issues need to start with an understanding of consumer attitudes and preferences. Consumers are interested in a consistent supply of safe, lean, attractive products of good eating quality. Significant progress has been made in improving carcass leaness and producers can influence the lean content of their pigs principally through choice of genetics and nutritional programs. Factors influencing carcass leaness are addressed in other presentations at this meeting. There are a number of other aspects of pig meat quality which are receiving increasing, attention, including the Pale Soft Exudative (PSE) condition and pork eating quality. Both of these aspects impact financial returns and/or consumer acceptability and are, therefore, of major importance to the swine industry.

The increased interest in the impact of genetics on meat quality stems mainly from two considerations. Firstly, there is concern that current selection programs which emphasize growth and carcass composition may produce a correlated deterioration in meat quality. In addition, the potential to select directly for improved meat quality is receiving increased attention. Both of these areas will be addressed in this paper.

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Correlated Changes in Eating Quality

Great strides have been made in improving carcass lean contents in pigs and a major part of this improvement results from successful genetic selection schemes. Arguably the biggest changes have occurred in Europe where price incentives to produce lean pigs have been high. For example, in the United Kingdom (UK) backfat depths have been approximately halved over the last 25 years. At present, the average backfat thickness in the UK (measured at the P2 position) is around 11mm and a significant number of commercial carcasses have fat depths below 6mm (MLC, 1994). Products from such pigs meet consumer requirements in terms of leaness but concerns have been raised about the eating quality of meat from such lean animals. There have been few attempts to directly estimate correlated changes in eating quality as a result of selection for increased carcass lean content. Most studies that have investigated the eating quality of meat from lean compared to fat carcasses and have selected extreme samples from commercial slaughter plants. One such study carried out under UK conditions compared meat from carcasses with 8 and 16mm P2 backfat (Wood et al., 1986). The results from this comparison are summarized in Table 1 which shows a small advantage in juiciness for the fatter animals but little difference between the fatness levels for other aspects of eating quality or overall acceptability suggesting little cause for concern over the eating quality of meat from leaner pigs. Given that the intramuscular fat (IMF) contents of pigs from the fat group (<1%, Table 1) was considerably lower than levels in most US pigs, these results also suggest that poor eating quality as a result of low IMF is unlikely to be a problem in the US in the foreseeable future. However, work at the University of Illinois (DeVol et al., 1988) has suggested a threshold level for IMF of at least 2.5 to 3% for optimal eating quality, which is considerably higher than found in most UK studies and further research is needed to clarify the association between IMF and eating quality across a wide range of IMF levels.

Warkup and Kempster (1991) have proposed a model for eating quality in which increases in fatness and/or lean growth rates result in increased tenderness and juiciness. Modern genotypes are both leaner and have higher lean growth rates and, according to the proposed model, would show minimal change in eating quality compared to more traditional lines of pig. To date, however, the interaction between lean growth rates and fatness in terms of eating quality has not been established.

Breed Variation in Eating Quality

Breed comparisons have been carried out for many years but it is only relatively recently that meat quality, and particularly eating quality, has been included in such studies. In Europe, in recent years, attention has been focused on the Duroc breed and claims of enhanced eating quality for this genotype compared to other European breeds and lines. Several studies have now been published comparing the Duroc with white lines and a number of these have shown a significant eating quality advantage for the Duroc, which has been attributed to the higher IMF levels for this genotype (Ellis et al., 1995a). Another breed with high IMF levels that has received considerable attention is the Meishan. An early study carried out in France suggested a substantial eating quality advantage for the Meishan compared to more conventional breeds (Touraille et al., 1989). Data from more recent studies

carried out in the US (Lo et al., 1992) and the UK (Ellis et al., 1995b) does not support the concept of better eating quality for Meishan crosses, with the American study actually finding that Yorkshires produced better eating quality than the Chinese genotype.

The dilemma with trying to interpret data from breed/genotype comparisons is illustrated by a recent experiment carried out at the University of Illinois (Ellis et al., 1995c). In this study, four genotypes which varied in IMF content were compared in a factorial experiment that also investigated post-mortem ageing time (2, 9 and 16 days) and endpoint cooking temperature (60, 70 and 80°C). The results of this study are summarized in Table 2. There were no practically important treatment interactions so only the main effect means are reported. Ageing the meat for 9 and 16 days produced improvements in tenderness and juiciness. In addition, increasing endpoint temperature produced a substantial deterioration in eating quality, highlighting the importance of cooking on eating quality. In terms of the genotype comparison (Table 2), the genotype with the highest IMF levels (G2) produced the best eating quality, particularly in comparison with the genotype with the lowest IMF (Gl). However, G4 which had relatively low levels of IMF produced meat that had significantly better eating quality than Gl and was similar in terms of shear force to G2. This suggests that IMF was not responsible for all of the genotypes differences observed in this study.

The results of a large scale comparison of US genotypes has recently been published (NPPC, 1995) and the eating quality component of this work is summarized in Table 3. Again, there is a general association between IMF levels and eating quality with those genotypes with high IMF levels giving the better results, although the genotype differences were relatively small. Interestingly, this work has stimulated interest in the Berkshire breed for its desirable eating quality.

In conclusion, the results of a relatively large number of recent studies comparing breeds/genotypes for eating quality show some advantage for high IMF genotypes. However, as well as differing in IMF levels genotypes show variation in many other components of muscle and fat which potentially can impact eating quality. For example, there is evidence of genotype variation in lean and fat growth rates, muscle fiber types, fatty acid composition of IMF, and the amount and structure of the connective tissue. All of these components can potentially influence pig meat eating quality and more fundamental studies are required to quantify the relative contribution of these factors to genetic variation in quality.

Single Genes Affecting Meat Quality
Halothane Gene

Although this gene has been known about for a considerable time and a significant amount of research has been carried out, interest in it has been rekindled in recent years in the US. There are two major reason for this. Firstly, the emergence of payment schemes that reward carcass leaness has prompted producers to look for techniques to produce leaner pigs. Secondly, the development of a definitive DNA test (the Hal-1843 test; Fuji et al., 1991; Otsu et al., 1991) that rapidly identifies all three halothane genotype (reactor [nn], negative [NN], and carrier [Nn]) has greatly facilitated work in this

areas. In particular, for the first time it has allowed carrier and negative pigs to be identified rapidly and has led to the development of more precise experimental approaches to quantify the differences in performance between these two genotypes. We have recently completed an experiment where carrier boars were mated to negative females with the resulting litters being comprised of approximately equal numbers of carrier and negative pigs which were compared for growth, carcass, and meat quality characteristics (Leach et al., 1995). The results of this comparison are summarized in Table 4 where they are compared with another study carried out at this center (Ellis et al., 1995) and results from the NPPC Terminal Line Program (NPPC, 1995).

The conclusions that can be drawn from these studies are that carrier animals have higher dressing percent and carcass lean contents than negatives but that meat from carriers tends to be paler and have a higher drip loss. From these results (Table 4), the impact of the carrier on eating quality appears to be relatively small. The study of Leach et al. (1995) also suggested an advantage for carriers in terms of feed conversion efficiency and there are other reports in the literature to this effect.

There is considerable debate over the most appropriate strategy to adopt with the Halothane gene with the choice being between exploitation of its advantages to the producer versus elimination. Although there may be some short term advantage from this gene, in the longer term, with the increasing emphasis on and importance of meat quality, the disadvantages of the gene may outweigh its advantages and elimination may be the most appropriate strategy.

Acid Meat Gene

A single gene with a large effect on meat quality that has been discovered more recently than the Halothane gene is the so-called "acid meat gene" which is also referred to as the Rendement Napole or RN gene. This gene was first identified in France in Hampshire populations and, to date, the gene has only been found in this breed. Monin and Sellier (1985) reported on a condition in Hampshires which resulted from a greater fall in muscle pH post mortem leading to low ultimate muscle pH levels. This meat was paler and wetter than normal and gave a marked decrease in processing yields for hams, as a result of increased water loss during cooking. The effect of the gene appears to be related to increased glycogen levels in the muscle at slaughter coupled with a greater glycolytic potential in the muscle. This results in more extensive post mortem glycolysis and lactic acid production and a lower pH (Monin and Sellier, 1985).

Further studies (Le Roy et al., 1990; Fernandez et al., 1992) have suggested that the acid meat effect can be attributed to a dominant gene and that the frequency of the dominant allele which is responsible for the excessive drop in pH may be as high as 0.5 in some Hampshire populations. This gene has recently been mapped to chromosome 15 (Milan et al., 1995) and a microsatellite marker has been identified which is linked to the gene.

Is the RN gene present in US Hampshire population? Although there is no direct evidence at present that it is, the recent findings from the NPPC genetic evaluation program (NPPC, 1995) of a lower ultimate pH for Hampshire-sired pigs compared to the other genotypes evaluated suggest that it probably is.

The decision on what action to take with the RN gene is more straightforward than with the Halothane gene. There appear to be no production or carcass advantages associated with the gene and, therefore, elimination of the unfavorable allele is the most appropriate course of action. The fact that the undesirable allele appears to be dominant will also make total elimination easier and quicker than with a deleterious recessive gene. This approach would be greatly facilitated if a reliable DNA based test was available. Unfortunately, this is not the case although there is every expectation that an appropriate test will be developed in time. Attempts to eliminate the dominant allele at present must use genotyping based on determination of the glycolytic potential of muscle samples which should allow the allele frequency to be reduced relatively rapidly.

A Gene for Intramuscular Fat?

The presence of a single gene in pigs associated with high intramuscular far (IMF) levels has been suggested by a study from Holland (Janss et al., 1994) which examined the variation in IMF in F2 crosses between Meishan and Dutch genotypes. IMF levels are higher in Meishans compared to improved breeds (Lo et al., 1992), suggesting that single genes affecting IMF may be segregating in the Chinese breed. Although the IMF gene has not been located and identified, such a finding would be of considerable benefit to the swine breeder. It would allow IMF levels to be manipulated more quickly and easily than with conventional techniques and may allow IMF levels to be increased independent of carcass fat levels.

A significant research effect is underway at a number of research centers in Europe and North America, including the University of Illinois, to identify genes associated with economically important traits in swine and other species. No doubt this will lead to the identification of more single genes with large effects on meat quality. As well as providing a means to select for improved meat quality, such findings can also provide an understanding of gene action and basic physiological and metabolic mechanisms controlling quality aspects and are likely to result in the development of management techniques, both pre- and post-slaughter, to improve meat quality.

Direct Selection for Improved Pig Meat Quality

A number of important meat quality traits appear to have moderate heritabilities (Cameron, 1990; de Vries et al., 1993) and could be included in selection objectives and indexes with reasonable expectation of making genetic improvements in meat quality. At present, however, there are major

limitations to such an approach. Firstly, measurement of meat quality in the live animal is difficult or impossible at the present time. In addition, selection pressure, and therefore selection response, will be reduced for other economically important traits which are being selected for in the index. However, selection programs have been very effective at reducing backfat levels in swine and, ultimately, an optimal level will be reached at which stage the opportunity to select for other traits is likely to increase. In addition, non-invasive techniques to measure quality components in the live animal are under investigation and developments in this area would make direct selection for improved pig meat quality practically more feasible.

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Table 1. *Influence of backfat thickness on eating quality of pork loin chops*[1]. *(from Wood et al., 1986)*

	Fatness (backfat thickness, P2, mm)		
	Lean (8mm)	Fat (16mm)	SED[2]
Intramuscular fat (%0	0.55	0.96	0.037***
Tenderness	1.0	1.1	0.37
Juiciness	1.0	1.3	0.07**
Flavor liking	1.5	1.7	0.15
Pork flavor	0.6	0.9	0.14
Overall acceptability	0.7	1.0	0.23

[1] Evaluated using a 15-point scale: -7 to +7; lower values = poorer quality.
[2] Standard error of the difference (SED).
* P< 0.05; ** P<0.01; *** P<.001.

Table 2. Effect of genotype, aging time, and endpoint cooking temperature on palatability characteristics of pork longissimus

	Genotype					Aging time (days)				Endpoint temperature (°C)			
Trait	G1	G2	G3	G4	SEM	2	9	16	SEM	60	70	80	SEM
Intra-muscular fat	1.54[a]	3.74[b]	2.18[a]	2.01[a]	0.30	-	-	-	-	-	-	-	-
Shear (kg)[e]	4.33[a]	3.61[b]	4.02[c]	3.67[b]	.06	4.07[a]	3.76[b]	3.90[b]	. 06	3.63[a]	3.89[b]	4.22[c]	.06
Cooking loss(%)	27.1	27.39	28.1	28.1	.43	28.3[a]	27.6[ab]	27.1[b]	.37	22.7[a]	26.9[b]	33.4[c]	.37
Juiciness[d]	8.1	8.8	8.3	8.3	.10	8.2[a]	8.2[a]	8.6[b]	.09	9.7[a]	8.2[b]	7.2[c]	.09
Tenderness[d]	8.4[a]	9.6[b]	8.7[c]	9.3[d]	.08	8.8[a]	9.0[ab]	9.2[b]	.10	9.6[a]	8.9[b]	8.5[c]	.10
Off-flavor[d]	14.9	14.9	14.9	14.9	.03	14.9	14.9	14.9	.02	14.9	14.9	14.9	.02

[abc] Means in the same row within the same factor with a different superscript differ (P < .05).
[d] Sensory measurements use a 15 cm structured line scale with 0 cm being extremely dry, tough, and intense off-flavor; and 15 cm being extremely moist, tender and no off-flavor.
[e] Warner-Bratzler shear force measurements taken on 1.3 cm diameter cores using an Instron machine.
SEM = standard error of the means.

Table 3. *NPPC Terminal Sire Line Comparison - Eating Quality Results (NPPC, 1995)*

	Lipid content[1] (%)	Shear Force (kg)	Juiciness[2]	Tenderness[2]
Berkshire	2.41[bc]	5.74[ab]	3.4	3.50[a]
Danbred HD	2.33[c]	5.81[ab]	3.4	3.45[ab]
Duroc	3.03[a]	5.65[a]	3.3	3.38[ab]
Hampshire	2.57[b]	5.86[ab]	3.4	3.36[ab]
NGT Large White	2.15[c]	6.09[c]	3.4	3.16[c]
NE SPF Duroc	2.71[ab]	5.78[ab]	3.4	3.36[ab]
Newsham Hybrid	2.25[c]	6.12[c]	3.3	3.25[bc]
Spot	2.35[c]	5.92[bc]	3.3	3.16[c]
Yorkshire	2.33[c]	6.13[c]	3.4	3.26[bc]

[1] Means in the same column with different superscripts are significantly different ($P < .05$)
[2] Trained sensory panel evaluation of cooked loin based on a 1-5 scale, with higher scores indicating more tender, juicier meat.

Table 4. *Comparison of differences between Halothane carrier (Nn) and negative (NN) pigs from three US studies (expressed as Nn-NN).*

	Leach et al. (1995)	Ellis et al. (1995)	NPPC (1995)	
			Difference	Genotype range
Daily feed intake (kg)	-0.22		-	
Daily gain (g)	+10		+5	
Gain:Feed	+0.03		-	
Dressing percent	_0.90		+0.38	
Carcass lean, %	+1.3[1]		+0.6	-0.8 to +3.1
Backfat thickness (cm):				
10th rib	+1.0	-1.7	0	
Last rib	0	-1.0	+1.0	
Last lumbar	0	+2.6	+0.50	
Loin eye area (cm^2)	+1.4	-1.3	+1.9	+0.3 to +5.9
Longissimus:				
Color score	-0.5	-0.2	-0.15	-0.5 to +0.1
Firmness score	-0.7	-0.3	-0.20	-0.1 to -0.6
Marbling score	-0.5	0	-0.21	-0.1 to -0.5
Drip loss (%)	+1.8	+0.2	+0.48	+0.7 to +3.9
Minolta reflectance	+3.7		+1.7	
Hunter L*		+1.0	+1.7	
Lipid content (%)	-0.30	-0.3	-0.33	-0.04 to -1.18
Cooking loss (%)	+1.5	+0.4	-0.4	
Shear force (kg)	0	-0.1	+0.5	-0.08 to 0.08
Juiciness	-0.3	-0.4	-0.09	
Tenderness	-0.1	-0.3	-0.28	
Flavor	-0.1	0	+0.02	

[1]Fat-free lean percentage.

USING THE TOOLS OF TECHNOLOGY FOR GENETIC IMPROVEMENT OF SWINE

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Introduction

Considerable progress has been made in improving swine production through the application of numerous biological technologies. However, improvements are still needed in the areas of product composition and production efficiency, especially with regard to growth, disease resistance, lactation and reproduction. The attainment of such advancements will depend heavily on our ability to quantify desirable traits, to identify genetic markers linked to gene(s) responsible for those traits, to select or "re-design" populations of superior individuals and then to propagate those animals. The integration of recombinant deoxyribonucleic acid (DNA) technologies into this scheme has been and will continue to be an important aspect of future advances.

Existing and developing technologies which are associated with genetic improvement, selective breeding and genome manipulation include phenotypic evaluation and selection, marker-assisted selection, genotyping, artificial insemination, embryo transfer , embryo manipulation, gene transfer and cloning. This paper will examine the potential utility of these technologies in developing strategies for genetic improvement of swine.

Integration of Classical and Molecular Genetics

Today's swine producers are under intense pressure to enhance growth rate, reduce carcass fat and increase the efficiency of nutrient conversion to lean tissue. Present improvements in these areas have been based on development and application of quantitative statistical models to evaluate and predict genetic gain according to Mendelian inheritance. These quantitative methods have allowed greatly accelerated genetic progress in livestock. Furthermore, we have expedited our selection efforts by introducing genetics from exotic (non-U.S.) breeds of swine, such as Pietrain and Meishan, into our more traditional pig breeds. Importation of exotic germplasm offers the opportunity to increase genetic variation from which one can select leaner and more efficient animals. The most rapid genetic progress will be provided by placing superior genotypes into our production herds

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Identification and quantification of desirable traits are critical if objective progress is to be made in improving swine genetics. Selection is an important method for altering gene frequencies to improve livestock for a specific purpose(s). Practically, it is defined as the process by which certain individuals in the population are identified and preferred over others for production of the next generation. Selection is classified into two general types, natural and artificial. Natural selection is shaped by the forces of nature and artificial selection is shaped by the conscious efforts of man. Selection does not create new genes, but increases the frequency of desirable genes in the population and decreases the frequency of less desirable genes.

There are several important aspects of selection. First, a desirable trait must be identified, such as litter size, feed efficiency, disease resistance, growth rate, reproduction and lactation performance. Second, genetic tests must be developed and used to identify superior individuals in the population. Third, the information obtained from the testing must then be evaluated and ranked to enable selection of superior individuals to be used as breeding animals for the next generation. Offspring resulting from these matings are then in turn subjected to testing and evaluation themselves.

Quantitative traits (such as litter size, growth rate and carcass composition) may be controlled by hundreds of genes. If one calculates the potential combinations of allelic (or variant) genes for such a trait, the number of genetic combinations is astronomical. With only 20 heterozygous genes there are approximately 3.5 billion genotypes in the gametes of such an individual (Taylor and Bogart, 1988). Therefore, the ability to screen and select the appropriate individuals as breeding stock for the next generation is critical if we are to maintain or increase our rate of genetic progress. It has been estimated that if we only use present testing and selection procedures our rate of projected genetic improvement will plateau in about 30 years (Figure 1, panel A, from Wheeler and White, 1993). Further, advancement due to molecular genetics is a "stair-step" phenomenon that makes progress in discrete increments (Figure 1, panel B). As molecular genetic technology is developed, a rapid improvement in specific production traits occurs. Once the maximum benefit from newly developed technology is realized, projected genetic gain reaches a plateau. During the plateau there is no demonstrable improvement until the next technological breakthrough when we see another abrupt increase in genetic progress. The potential contribution of molecular genetics is remarkable but is, unfortunately, limited by the frequency of technological developments. In order to achieve the maximum rate of genetic progress we must utilize a combination of both quantitative and molecular genetics. This combination will increase the rate of genetic progress faster than either quantitative or molecular genetics will alone (Figure 1, panel C). The contribution from these genetic disciplines will likely be integrated with molecular genetics providing tools and mechanisms to understand the underlying genetic processes and quantitative genetics providing the systematic and objective applications of these tools and mechanisms at the population level (Kennedy et al., 1990). Furthermore, advances in molecular genetics have and will continue to identify new questions and problems for quantitative genetics. Similarly, quantitative genetics will be essential for the application of molecular technology to livestock selection programs. An example of how this combination of technologies may be used is in the selection of breeding stock. Molecular genetic markers will allow rapid prediction of potential breeding animals. This will enable the selection

of breeding stock at birth or even at the embryo stage. These individuals can then enter the breeding herd at puberty and make a positive impact on performance very quickly. These individuals can be selectively bred and their offspring, in turn, can be evaluated (via quantitative and molecular methods) and selected. Superior offspring will replace their parents in the breeding herd. Using such a scheme we may achieve more rapid genetic progress because superior individuals are identified early and only these animals enter quantitative testing and subsequent further selection.

Molecular Genetic Technologies

Gene Mapping

The genome of an animal is the complete set of genetic instructions that determine what the animal will be, how it will function, what it will look like, how it will reproduce, how it will grow, what diseases it will be susceptible or resistant to, how long it will live and how it will respond to its environment. A genetic map like any other map is essentially a set of locations or coordinates. These locations identify a specific place where each one of the genes or DNA sequences are specifically located in the genome.

Gene mapping is the technology whereby the location of a gene or DNA sequence is described. Practically, it is the location of genetic material involved in a trait(s) of interest to livestock producers. There are a number of types of genetic maps which describe gene locations in different ways. One type of map is a *physical map* where genes or DNA sequences are assigned directly to a chromosome or a region of a chromosome. This localization may even be to the level of the specific nucleotides (molecules) that make up the DNA. A second type of genetic map is a *linkage map* in which a gene or DNA sequence is described by its relative location to a readily identifiable reference point or *genetic marker* along the chromosome. The linkage map is based on the likelihood that the DNA of interest and the genetic marker will remain together, or linked, during meiosis. Meiosis is the process of cell division that results in the production of sperm and ova. One additional type of genetic map that has been very useful is the *comparative gene map*. This uses genes mapped in other species including the human and relies heavily on the conservation of DNA sequences across mammalian genomes. Comparative mapping has been used to identify conserved genetic linkage groups among species.

There are several approaches that can be used to identify major genes (loci) that control quantitative and/or economically important traits. One such approach employs the selection of genes which may be directly involved in the trait of interest, the so-called candidate genes. This method uses expressed DNA sequences which code for specific proteins, such as milk caseins, muscle myosin, hormones, growth factors or their receptors. These sequences are used because they control physiological processes underlying these quantitative trait loci (QTL) and/or economically important trait loci (ETL) (Schook et al., 1994). A second approach utilizes random genetic markers that are highly polymorphic (having many forms in a population of animals) and present in a single copy in the DNA. These are known as microsatellite markers. The identification, sequencing and assignment of microsatellites to chromosomes provide

development of unique, genetic landmarks which can be used for identification of QTL's and ETL's. Recently, the first swine microsatellite linkage map was constructed (Rohrer et al., 1994).

The location of genes affecting important traits can be identified by their association with the polymorphic genetic markers (Schook et al., 1994). Many genes that have been mapped in the human genome may provide markers in the swine genome for quantitative traits. In the human, 72 different genes have been identified that control growth (McKusick, 1989). Of these 72 genes, 29 encode for growth factors or growth factor receptors. The remainder are genes which encode for proteins that influence or modify these growth factors and/or their receptors.

Our group has recently identified genetic markers for a number of candidate genes which are potentially involved in growth, reproduction and disease resistance in swine. These include protein kinase C_{ϵ}, low-density lipoprotein receptor, cholesterol-7α-hydroxylase, interleukin-6, cholesterol-7α-hydroxylase, α-lactalbumin, HMG Co-A reductase, nebulin, growth hormone, insulin-like growth factor I, and nerve growth factor (Allen and Wheeler, 1993; Davis et al., 1993; Shalhavet et al., 1993; Davis et al., 1994; Bleck et al., 1995; Davis et al., 1995; Atac et al., 1995; Conrad et al., unpublished; Gilette et al., unpublished; Conrad et al., unpublished).

The present emphasis of biotechnology in animal production stresses the need to integrate molecular genetics into the identification of major genes affecting reproductive performance, growth and development, disease resistance and lactation. Therefore, the identification and mapping of genetic variants which affect quantitative traits will increase the rate of genetic improvement of livestock.

Genetic Screening and Marker Assisted Selection (MAS)

General

Once genetic markers which are associated with QTL's or ETL's have been identified then it is necessary to screen animals to determine the frequency of the allele or marker in the population and use these markers for marker assisted selection. Screening is performed on isolated DNA which may be obtained from a variety of tissues including blood, semen, hair, ear notches, tail, skin, milk and embryonic cells. Once the animals are screened, the pigs with the desired genotype or allele can be selected.

One method to select these animals is to predict the genotypes of embryos by microbiopsy of embryonic cells and use the polymerase chain reaction (PCR; Mullis and Faloona, 1987) to amplify specific regions of DNA. Recent development of PEP (Zhang et al., 1992), a method that increases the available number of copies of all genes for amplification by PCR, allows screening of embryonic biopsies for genotypes at multiple loci simultaneously. The ability to accurately predict genotypes of preimplantation porcine embryos could facilitate marker assisted selection for traits of economic importance. We have recently shown the feasibility of predicting

genotypes of individual preimplantation embryos by using specific DNA amplification techniques known as polymerase chain reaction and restriction fragment length polymorphism (PCR-RFLP) analysis. These allow genotyping of multiple economically important genes (or loci) while maintaining embryo viability for production of live young (Wheeler et al., 1995, Jarrell et al., 1994, 1995). Another practical application of this methodology is sex determination of embryos using Y-specific chromosome sequences (Fajfar-Whetstone et al., 1993).

Unfortunately, the number of genetic markers which have been associated with quantitative traits are limited in swine. However, several markers which may have potential economic impact on swine production have been identified. These include the ryanodine receptor locus, SLA haplotypes, the K88 locus, the RN locus, the transferrin locus, the GPI and PGD loci, the GH and IGF-I loci, the ESR locus and the α-lactalbumin. These are briefly discussed below (excerpted from Miller, 1995 with permission).

Ryanodine Receptor (formerly the Halothane Sensitivity)

The mutated ryanodine receptor locus is responsible for porcine stress syndrome (PSS). PSS is a major economic problem which costs the pork industry millions of dollars each year. Pigs exhibiting PSS have shown a higher incidence of pale, soft, and exudative pork (PSE). PSE poses another economic problem because of the poor quality of the meat. In the past pigs had been genotyped for this disorder by the administration of halothane gas. Fujii et al. (1991) developed the HAL-1843 DNA test. This has enabled a fast, accurate way of determining genotypes, including the ability to decipher between the homozygous recessive (nn) and heterozygous individuals (Nn). The DNA test has facilitated studies to evaluate the commercially applicable quantitative effects of this gene.

Porcine Major Histocompatibility Complex

The porcine major histocompatibility complex (MHC), also called the swine lymphocyte antigen (SLA) system, has major effects on cell recognition within the immune system and immune system responses. Gautschi and Gaillard (1990), Jung et al. (1989), and Rothschild et al. (1986, 1990) have shown associations between different SLA haplotypes and quantitative traits including birth and weaning weights (Rothschild et al., 1986) and litter size at weaning (Gautschi and Gaillard, 1990).

K88

The K88 antigen is a filamentous surface antigen that promotes the adhesion of enteropathogenic *Escherichia (E.) coli* to the intestinal epithelium in piglets (Clamp, 1991). Any pig which lacks the intestinal receptor for K88 has shown a resistance to both experimentally and naturally induced infection of K88-positive *E. coli* (Edfors-Lilja et al., 1986).

RN (Rendement Napole) or Acid-Meat

During the processing of pork, differences in pork quality become evident. Differences in pork

quality can be identified by many properties such as water holding capacity, color, marbling, firmness, shear force and processing yield. These properties can be altered by post-mortem changes in pH (Warris and Brown, 1987). Monin and Sellier (1985) found that Hampshires have a normal decrease in post-mortem pH, however the level of post-mortem pH is much lower than other lines of pigs. This low ultimate pH results in lower processing yields.

Transferrin

Transferrin is a serum protein which has been associated with embryo loss in pigs due to a decreased chance of survival *in utero* (Imlah, 1970). The lack of homozygotes in the offspring showed the possibility of embryo mortality due to genotype.

Glucosephosphate Isomerase (GPI) & Phosphogluconate Dehydrogenase (PGD)

Growth and carcass traits in swine have been associated with alleles of GPI and PGD (Clamp, 1991). The A allele of GPI has shown an increased average daily gain and more lean gain per day. The PGD B allele was associated with a higher muscle firmness score than the A allele.

Growth Hormone (GH) & Insulin-like Growth Factor (IGF-1)

The exogenous effects of growth hormone on pigs demonstrated by Chung et al. (1985) and Hacker et al. (1993) have shown the ability to enhance growth and leanness. One study has attempted to associate polymorphisms of the growth hormone to economically important traits in swine (Casas-Carrillo et al., 1994). They found no associations to growth traits, but did detect an association to loin-eye area. The effects of GH are mediated by insulin-like growth factor-1 (IGF-1), which has been shown to be directly associated with growth in mice (Pell and Bates, 1989). Casas-Carrillo et al. (1994) also reported tentative associations of an IGF-1 marker to growth in swine.

Estrogen Receptor (ESR)

Rothschild et al. (1994) reported an association of a polymorphism in the ESR gene with a major affect on litter size in pigs. They found a difference of 1.4 more pigs born per litter between the two homozygous genotypes. Differences in average daily gain and back fat were not detected between any of the genotypes.

α-Lactalbumin

A genetic marker in the gene for the porcine milk protein α-lactalbumin has been associated with maternal characteristics in various lines of swine. Animals that were selected for maternal characteristics had a higher frequency of the A allele than did animals that had been selected for paternal or terminal cross traits (Roberts et al., 1995).

Genome manipulation

General

The capability to insert exogenous genes (transgenes) into organisms and establish their stable integration into sperm or ova (germ-line) has been a major technical advance in agriculture. Production of transgenic livestock provides for directed genetic changes in cattle, swine, sheep and goats. This is a more focused methodology but in essence not different from crossbreeding or genetic selection in its result. Practical applications of transgenic livestock include enhanced reproduction, growth, milk composition, milk production and disease resistance.

Transgenic animals are individuals that have incorporated a **trans**ferred "cloned" **gene,** known as a *transgene*, into their genome that may be passed to their offspring (Wheeler, 1991). Transgenic animals are produced by inserting the foreign DNA (transgene) into embryos prior to implantation. The transgene is able to integrate into the chromosomes or genome and subsequently be expressed in the resulting individual. The objective of this technology is to produce animals which have the transgene stably incorporated in their germ line. Such individuals are able to act as founder stock to produce many offspring that carry a desirable gene or genes. Transgenic animals have been produced by: 1) exposure of ova or embryos with recombinant retroviruses (Jaenisch, 1988); 2) microinjection of genes into pronuclei of fertilized ova (Gordon and Ruddle, 1981); and 3) injection of embryonic stem cells, previously transformed with a transgene, into the cavity of blastocysts (Robertson, 1987).

Pronuclear Injection

Microinjection of DNA into the pronucleus of a fertilized ovum has been the most widely used and successful method for producing transgenic swine (Brem et al., 1985; Hammer et al. , 1985; Wieghart et al., 1990). Briefly, fertilized one-cell embryos are removed from the donors, injected with DNA and transferred back into recipient females (Figure 2). Following the transfer, pregnant recipients will follow normal gestation and deliver term young. The primary advantage of microinjection of a transgene into pronuclei is the higher efficiency of generating transgenic animal lines (Rexroad and Pursel, 1988). Unfortunately, livestock species such as swine, have a much lower frequency (1-10%) of chromosomal integration of transgene DNA which makes production expensive (Rexroad and Pursel, 1988). Currently, using pronuclear injection methodology, the cost of producing **one** transgenic pig is about $25,000 (R.J. Wall, 1991, personal communication). To insure obtaining a pig that expresses the transgene, this figure may increase approximately 10-fold. Nevertheless, the production of a transgenic pig which has stably incorporated the transgene in its germ-line should allow for the recovery of production costs by the sale of superior offspring. Practically, however, reduction in this cost and improvement in the efficiencies of transgenic production are imperative if we are to readily utilize transgenic technology in swine production.

Once the transgene is inserted into the embryo, the embryo is then transferred to a suitable recipient female. Following the transfer, pregnant recipients will have a normal gestation and

delivery. Shortly after birth, the offspring resulting after gene transfer are examined for presence of the transgene in their genome by PCR or Southern blot analysis (Hammer et al., 1985). Pigs that have incorporated the transgene into their own DNA are transgenic and can then be used for subsequent evaluation with the ultimate goal of entering the production herd. In order to be of any practical utility in pork production the transgenes must be expressed and impart some particular advantage(s) over their non-transgenic contemporaries. Traditional progeny testing of these transgenic pigs will still be required in order to establish their superior characteristics.

Embryonic Stem (ES) Cells

Embryonic stem cells afford a potential alternative method to produce transgenic offspring (Robertson, 1987; Murray et al., 1988). This technology involves injection of embryonal cells into expanded blastocysts (approximately 7 days post-fertilization) to produce hybrid embryos composed of two or more distinct cell lines (Figure 3). These embryos are called "chimeras". Embryonic stem (ES) cells are derived from the inner cell mass of blastocyst stage embryos (Evans and Kaufman, 1981; Martin, 1981; Bradley et al., 1984; Robertson, 1987. These cells are able to produce all tissues of an individual animal. Once isolated, ES cells may be grown *in vitro* for many generations. This produces an unlimited number of identical cells capable of developing into fully formed adult chimeras (Evans and Kaufman, 1981; Martin, 1981; Bradley et al., 1984; Wobus et al., 1984; Robertson, 1987). These cells may then be transformed genetically (e.g. injected with foreign DNA) before being used to produce chimeric embryos (Thomas and Capecchi, 1987). When these transformed cells are incorporated into the gonads and participate in the production of sperm and eggs, the offspring that are produced by these chimeric individuals will be transgenic (Bradley et al., 1984; Robertson, 1987; 1991). It is not the individual that results originally from the chimeric embryo that is transgenic, but that individual's offspring. This is an important distinction in that the chimeric individual can act as founder stock to produce many offspring which carry the desirable gene(s). Results have shown that this method is effective for producing transgenic mice (Thomas and Capecchi, 1987; Capecchi, 1989; Robertson, 1991).

Embryonic stem cells have several distinct advantages for use in the production of transgenic individuals. The efficiency of transgenic animal production may be increased (Gossler et al., 1986; Rexroad and Pursel, 1988). Large numbers of these cells can be transformed *in vitro* with transgene DNA (Thomas and Capecchi, 1987; Capecchi, 1989; Robertson, 1991). Individual cell lines can then be isolated and derived from a single cell. These individual cell lines, once established, can be screened for incorporation of the transgene into the host DNA (Gossler et al., 1986; Thomas and Capecchi, 1987). Production of transgenics from DNA-transformed, individually derived and screened embryonal cell lines would allow large numbers of genetically identical animals to be established. These individuals would have the transgene integrated into the same place in the genome. This potentially could allow development of stable strains or lines of animals that all have the inserted gene at the same location. It may also eventually be possible to replace existing genes with genetically altered genes, via homologous recombination, rather than simply inserting new DNA into the genome at random (Thomas and Capecchi, 1987). Additionally, the combination of ES cell and nuclear transfer methodologies may allow for the rapid development of genetically identical animals with a targeted gene insertion.

Nuclear Transfer/Cloning

The use of nuclear transfer (or cloning) techniques will increase the number of potential offspring from a single female into the thousands and possibly the tens of thousands (Bondioli et al., 1990). The biological basis for nuclear transfer is that nuclei of embryonic cells, including ES cells, are totipotent or able to form any tissue in the fetus. Therefore, these nuclei may be transferred into a donor oocyte or egg and direct the development of the resultant individual (Fig. 4). If these nuclei are derived from an identical genetic background all the offspring produced will be identical or clones. Clones have only been produced by transfer of embryonic nuclei, none have been produced using the nucleus from any later stage cell types (Robl et al., 1987; Prather et al., 1987). The development ES cells from swine provides an additional source of embryonic nuclei which can be used in nuclear transfer protocols. The combination of transgenic ES cell and nuclear transfer methodologies should provide for the production of large numbers of genetically identical transgenic pigs.

Embryonic stem cell transfer

Nuclear transfer with ES cells as karyoplasts has only been reported on one occasion in mice (Tsunoda and Kato, 1993). Although blastocyst development was obtained, no live young were born. Implantation sites were detected but no fetuses were recovered. Similarly, nuclear transfer experiments with cells very similar to ES cells, embryonal carcinoma (EC) cells, have produced some morula and blastocyst development but no live mice (Modlinski et al., 1990). Therefore, little information is available regarding nuclear transplantation with ES cells.

Embryonic stem cell and nuclear transfer technologies are still experimental and a considerable amount of work remains before they are routine. Further, few laboratories are proficient at these procedures. Therefore, the projected cost of a cloned, transgenic porcine embryo is not yet known. Commercialization of this technology will enable selection pressure to be exerted upon females at an extent similar to that exerted currently on the male through artificial insemination (Wheeler and Campion, 1993).

Application of Transgenics in Swine Production

The production of transgenic swine has been instrumental in providing new insights into the study of the mechanisms of the action of genes implicated with having a role in the control of growth (Brem et al., 1985; Hammer et al., 1985; Seamark, 1987; Vise et al., 1988; Wieghart et al., 1990). There are numerous other potential applications of transgenic methodology to develop new or altered
strains of swine. Some of these are described below.

Improvement of Milk

Advances in genetic technology have made it possible to consider making substantial changes either in the composition of milk or in the production of entirely new products in milk. These changes have the ability to add value to, as well as increase the potential uses of milk. Through

genetic engineering it has become possible to produce any protein from any animal, plant or bacterial species in the milk of mammals. For example, it is possible to express milk proteins and other proteins of pharmaceutical value in the milk of mice, rabbits, pigs, goats and sheep (reviewed by Bremel et al., 1989). Advantages of the mammary synthesis of proteins include the ability of the mammary secretory cells to properly modify the protein so it is biologically active and then secrete the protein containing fluid (milk) in large quantities. Transgenic alteration of milk composition has the potential to enhance the production of certain proteins and/or growth factors that are deficient in milk (Wall et al., 1991). The improvement of the nutrient or therapeutic value of milk may have profound impact on survival and growth of newborn pigs.

The ability to increase animal growth or improve animal survivability through the modification of milk composition will depend on the capability of producing transgenic animals that produce a greater quantity of milk, a milk of higher nutrient content or a milk that contains a beneficial nutriceutical protein. The major nutrients in milk are protein, fat and lactose and the elevation of any of these components in milk would be associated with increased growth of the developing offspring. In swine 44% of the growth rate of the developing piglets can be attributed to milk yield and milk composition of the sow (Lewis et al., 1978). This high percentage of growth attributed to milk indicates the potential usefulness of this technology to the developing piglet. The benefit of increasing the nutrient content of milk or the level of milk production to aid the growth of the offspring will be limited to species or breeds of animals that are limited in growth by the lack of milk or nutrients contained in milk. In many production species such as cattle, sheep and goats the nutrients available to the young may not be limiting. However in swine one of the most important factors limiting piglet growth and eventually pig production is milk production (Hartmann et al., 1984). Methods that increase the growth of piglets during suckling result in an increase in weaning weights, a decrease in the number of days required to reach market weight, and thus a decrease in the amount of feed needed for the animals to reach market weight. These changes increase the efficiency of pork production and thereby increase the profitability of the animals.

A second mechanism by which the alteration of milk composition may affect animal growth is the addition or supplementation of beneficial hormones, growth factors or bioactive factors to the milk through the use of transgenic animals. It has been suggested that bioactive substances in milk possess important functions in the neonate with regard to regulation of growth, development and maturation of the gut, immune system and endocrine organs (Grosvenor et al., 1993). The over expression of a number of these proteins in milk through the use of transgenic animals may improve growth, development, health and survivability of the developing offspring. Some factors that have been suggested to have important biological functions in the neonate that are obtained through milk included IGF-I, EGF, TGFα and lactoferrin (Grosvenor et al., 1993).

Other properties that can be considered for modification are in the area of animal health. It has been shown that specific antibodies can be produced in transgenic animals (Storb, 1987). It might be possible to produce antibodies in the mammary gland that are capable of preventing MMA (mastitis-metritis-agalactia) or antibodies that aid in the prevention of animal diseases.

Modification of Growth

The production of transgenic livestock has been instrumental in providing new insights into the mechanisms of action of genes implicated in the control of growth. Transgenic mice, sheep and pigs have been used to examine postnatal mammalian growth. Growth hormone and insulin-like growth factor genes have been incorporated and expressed at various levels in these animals enabling the study of chronic expression of these hormones. Results have shown that increasing human growth hormone (hGH) leads to enhancement of growth and feed efficiency in swine, yet is accompanied by side effects such as increased incidence of arthritis and thickening of bone (Pursel et al., 1990). Similar increases in growth have been shown with the porcine growth hormone (pGH) gene but without increased arthritis and abnormal skeletal growth (Vise et al., 1988). Several other genes have also been introduced into transgenic livestock in an effort to alter growth. One strategy that was explored to address the problems associated with over-expression of growth hormone was to increase growth hormone production by increased stimulation of the pituitary. This was done by producing growth hormone releasing factor (GHRF) transgenic pigs. However, no significant increase in growth hormone was observed when this transgene was introduced in swine (Pursel et al., 1989). An alternative approach was to introduce the '*ski*' *oncogene* from chickens which had previously been shown to cause hypertrophy of numerous muscles while reducing body fat. This strategy has had limited success although muscle hypertrophy has been observed in some transgenic pigs (Pursel et al., 1992). Additional specific loci which may have some effects on altered growth patterns are the ryanodine receptor and *myo-D* genes. However, there are many more potential growth related genes for growth factors, receptors or modulators which have not been used, but may be of practical importance in producing transgenic livestock with increased growth rates and/or feed efficiencies.

Modification of Disease Resistance

The potential to increase disease resistance by introducing specific genes into livestock is a very interesting aspect of gene transfer. The identification of a single gene in the major histocompatibility complex (MHC) that was able to influence the level of immune response was instrumental in the recognition of the genetic basis of disease resistance/susceptibility (Benacerraf and McDevitt, 1972). We have realized, only in the last 20 years, the importance of selection for increased resistance to disease in our livestock. It is now known that there are many aspects of disease resistance or susceptibility in livestock that are genetically determined (reviewed by Lewin, 1989).

The application of transgenic methodology to specific aspects of the immune system should provide opportunities to genetically engineer livestock with superior disease resistance. However, little information exists regarding the roles of specific genes in the immune or other systems in the etiology of diseases with economic importance in livestock species (Ebert and Selgrath, 1991). Therefore, until there is sufficient information regarding the appropriate disease-related genes to manipulate, the production of transgenic livestock is probably premature.

One specific example where transgenesis has been applied to disease resistance in livestock is the production of swine that are resistant to influenza. Mice and mouse cell lines that contain the Mx+ protein are resistant to infection with influenza virus (Haller et al., 1981). The Mx gene has been microinjected into the pronucleus of porcine zygotes and has produced pigs that are resistant to influenza infection (Muller et al., 1992). This manipulation is an excellent example of how transgenesis may be used to increase disease resistance in livestock. The application of ES cell technology will enable the augmentation of beneficial alleles and/or the removal (via gene 'knock-out') of undesirable alleles associated with disease resistance or susceptibility. Potential areas of investigation include resistance to 1) parasitic organisms such as trypanosomes and nematodes; 2) viral or bacterial organisms such as bovine leukemia virus, pseudorabies virus, hoof and mouth virus, clostridium and streptococcus; and 3) genetic diseases such as DUMPS (deficiency of UMP synthase) and BLAD (bovine leukocyte adhesion deficiency). This is only a partial list as many other organisms or genetic diseases that decrease production efficiency may also be targets of genome manipulation via transgenic methodologies.

Propagation of Individuals with Superior Traits

Once superior pigs are identified by marker assisted selection or produced by genome manipulation, it becomes a process of propagating the desirable traits from these individuals into the next generation of offspring. This may be accomplished by either natural or artificial mating of animals. The primary method for improving swine is the use of genetically superior sires to produce offspring. Artificial insemination (A.I.) has been used in the swine industry for over 30 years to increase the frequency of desirable traits from superior sires (Aamdal, 1968). The primary advantage of artificial insemination is that genetically superior boars can be used much more extensively. Using diluted semen collected from fertile boars, it is possible to breed 1200-2000 females per year (Diehl et al., 1987). Conception rates from artificial insemination using fresh boar semen range from 70-86% (Uhlen, 1986) and ~55% with frozen semen (Larsson and Einarsson, 1976). Using this method, an individual boar or boars may have profound effects upon certain gene frequencies in the population. In 1985, it was estimated that greater than 6 million females were bred by artificial insemination worldwide (Crabo, 1991). The number of females bred by A.I. worldwide is likely much higher in 1995. Rapid progress may be made utilizing this technology in combination with quantitative genetics and perhaps in the future, with marker-assisted selection and genome manipulation.

In most domestic livestock species, it is difficult to get many offspring from a single superior female. Swine are the exception, with their ability to produce litters of eight to 12 pigs/litter twice per year. Embryo transfer procedures (Hancock and Hovell, 1962; Dzuik et al., 1964; Vincent et al., 1964) enable a genetically superior female, via the use of ovulation stimulating hormones and artificial insemination, to have several hundred offspring per year (Seidel, 1981). Nevertheless, the genetic impact by a female using embryo transfer is not as great upon the population as the impact of an A.I. boar which produces several thousand offspring. However, if the superior females are used to produce the boars that enter the A.I. stud, their influence can be quite dramatic. Embryo transfer may also be used to introduce or rescue valuable germplasm and propagate rare breeding animals such as Chinese Meishan swine.

Future

The overall goal is to increase production efficiency, especially with regard to reproduction, milk production or production of specific milk components, lean tissue growth with reduced fat content and decreased susceptibility to specific diseases. Significant progress will continue to be made in improving swine production through exploiting various technologies. More pork products are produced using fewer breeding stock than was envisioned even a decade ago. This pork is produced more efficiently and with less competition with man for high quality cereal grains. However, we still need to reduce fat content and increase production efficiency, especially with regard to lean tissue growth. In order to successfully attain these improvements we will profoundly test our ability to quantify desirable traits (quantitative genetics), to identify markers linked to gene(s) responsible for those traits (marker-assisted selection and gene mapping), to select or "re-design" populations of superior individuals (screening and gene transfer) and to propagate those animals (cloning, embryo transfer and artificial insemination). The incorporation of recombinant DNA technologies into this strategy will continue to be an important aspect of future advances. Furthermore, the production capability of genetically selected and/or genetically engineered swine will only be realized when their genetic potential is blended with appropriate environmental and management considerations.

In conclusion, there are a number of new and developing technologies that will have a profound impact on the genetic improvement of swine. The rate at which these technologies are incorporated into production schemes will determine the speed at which we will be able to achieve our goal of more efficiently producing pork which meets consumer and market demand.

Acknowledgements

The authors would like to thank their colleagues who have contributed to the work described, Laurie Rund, Michael Ellis, Lawrence B. Schook, Ron Feltes, Diana Bidner, Scott Hughes and Bill Fisher. The authors would like to give special thanks to Douglas Miller who allowed portions of his M.S. Thesis to be excerpted for this review.

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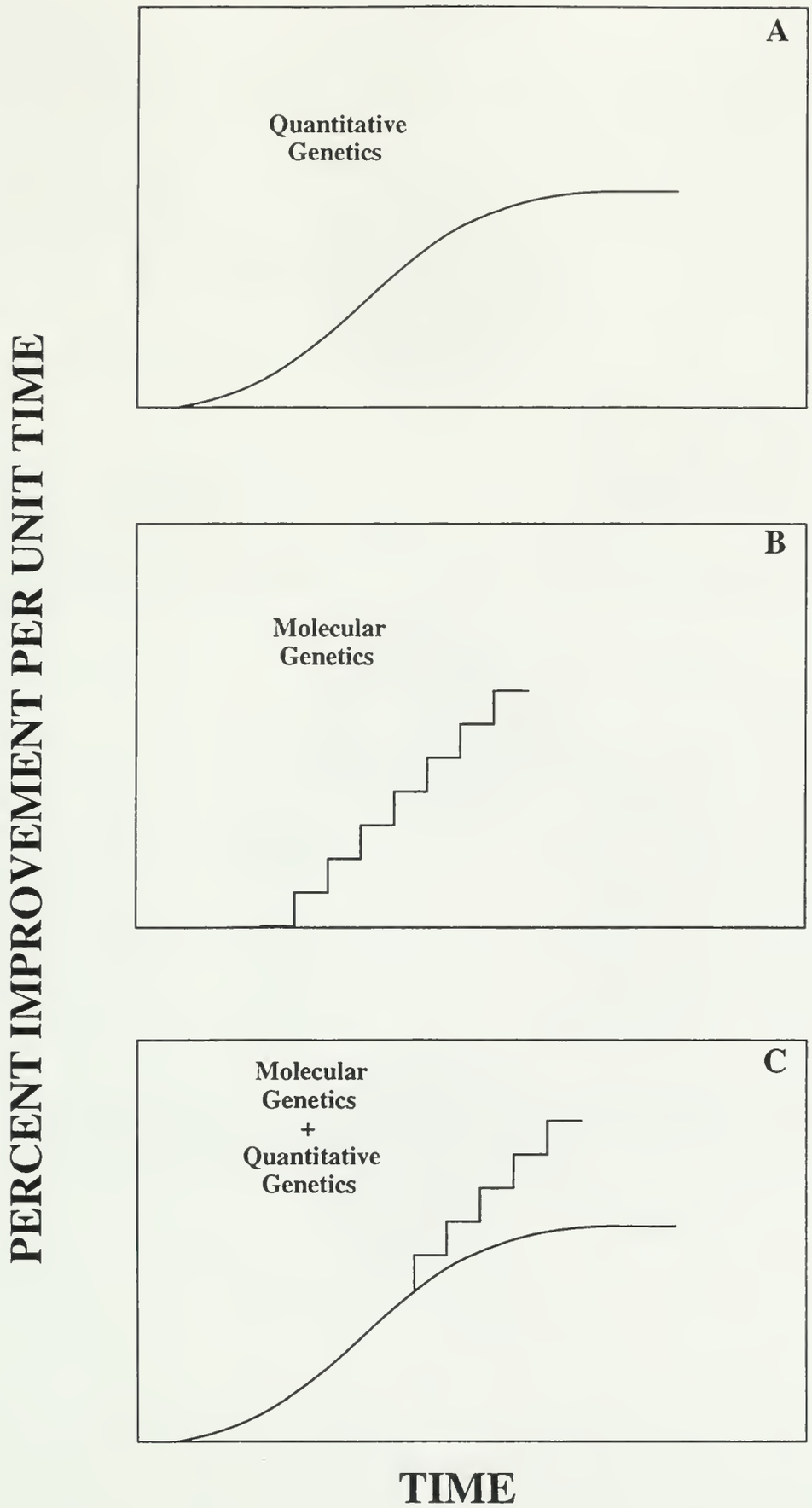

Figure 1: A schematic model of projected genetic progress for quantitative traits (i.e. carcass quality, growth rate, litter size, disease resistance or reproductive performance) in swine using the methodologies associated with quantitative genetics alone (Panel A), molecular genetics alone (Panel B) or a combination of both quantitative and molecular genetics (Panel C), see text for complete explanation.

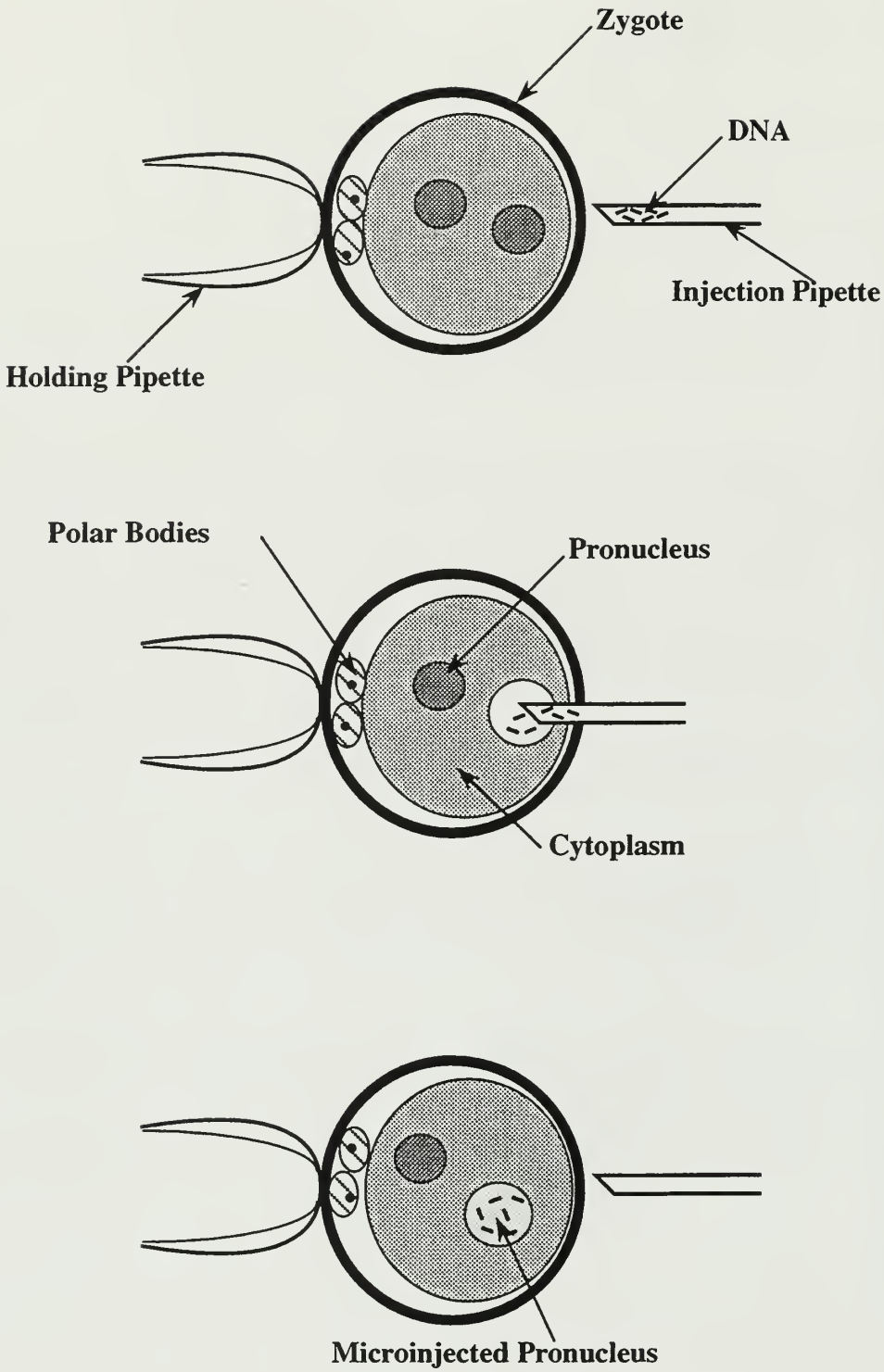

Figure 2: A schematic diagram of DNA microinjection into the pronucleus of a one-cell fertilized embryo (zygote). The zygote is grasped by a finely polished glass holding pipette (TOP). The DNA is injected into the pronucleus of the zygote (MIDDLE). The needle is withdrawn from the pronucleus and the embryo is released (BOTTOM). Ultimately, the injected embryo is transferred to a suitably prepared recipient.

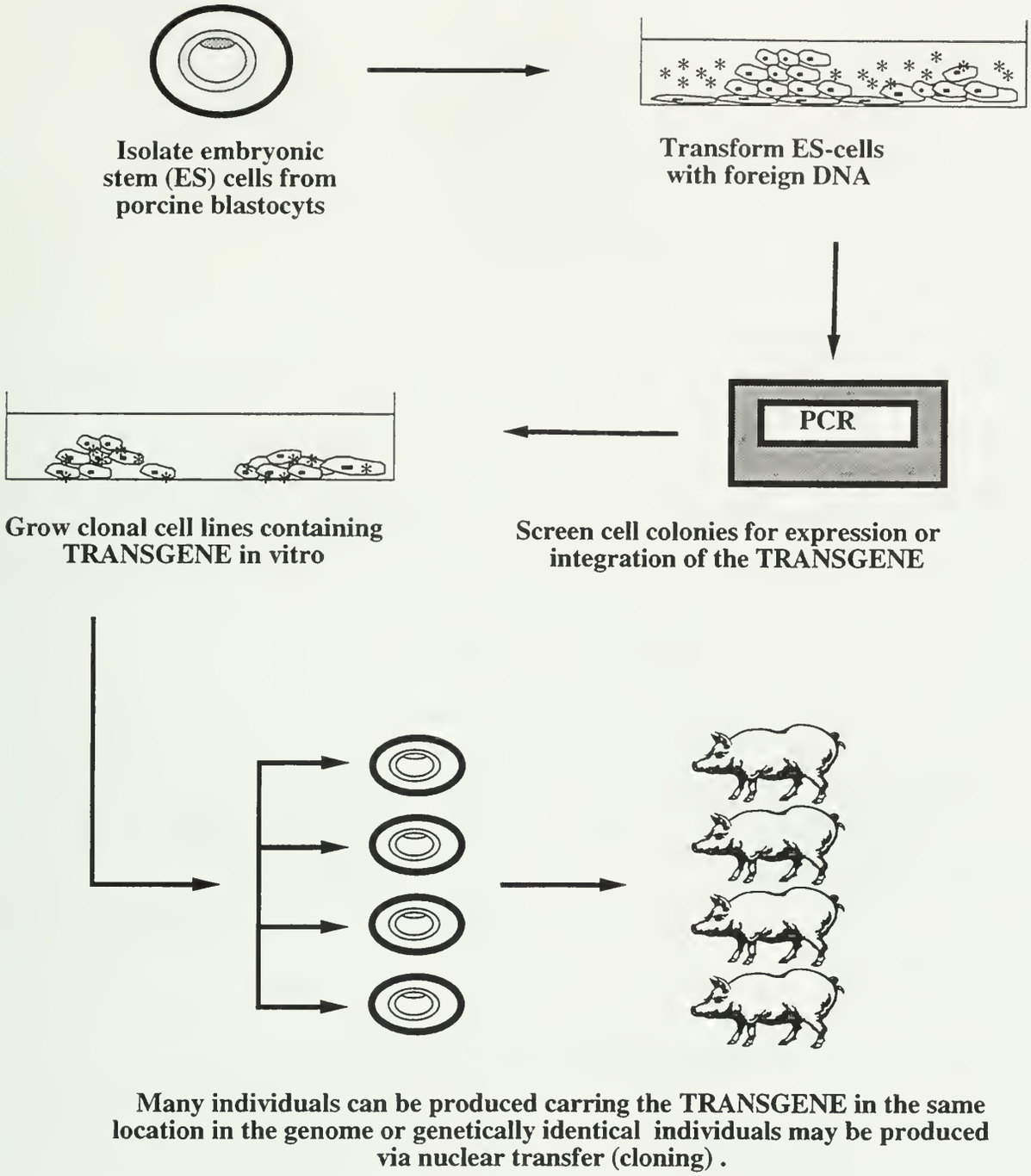

Figure 3: A schematic diagram of the methods used to produce transgenic swine with embryonic stem cells. ES-cells are isolated from a porcine blastocyst approximately 7-8 days post-fertilization. Once isolated, the ES-cells are transformed with 'foreign' DNA. Individual cell colonies are screened for integration by the polymerase chain reaction (PCR, method shown), screened for expression using a marker gene such as ß-galactosidase or by assay of the specific gene product. After the desired transformed ES-cell colonies are identified they can be grown to produce many cells containing the transgene. The transformed ES-cells may then be used to produce chimeras or in nuclear transfer programs to produce genetically identical swine.

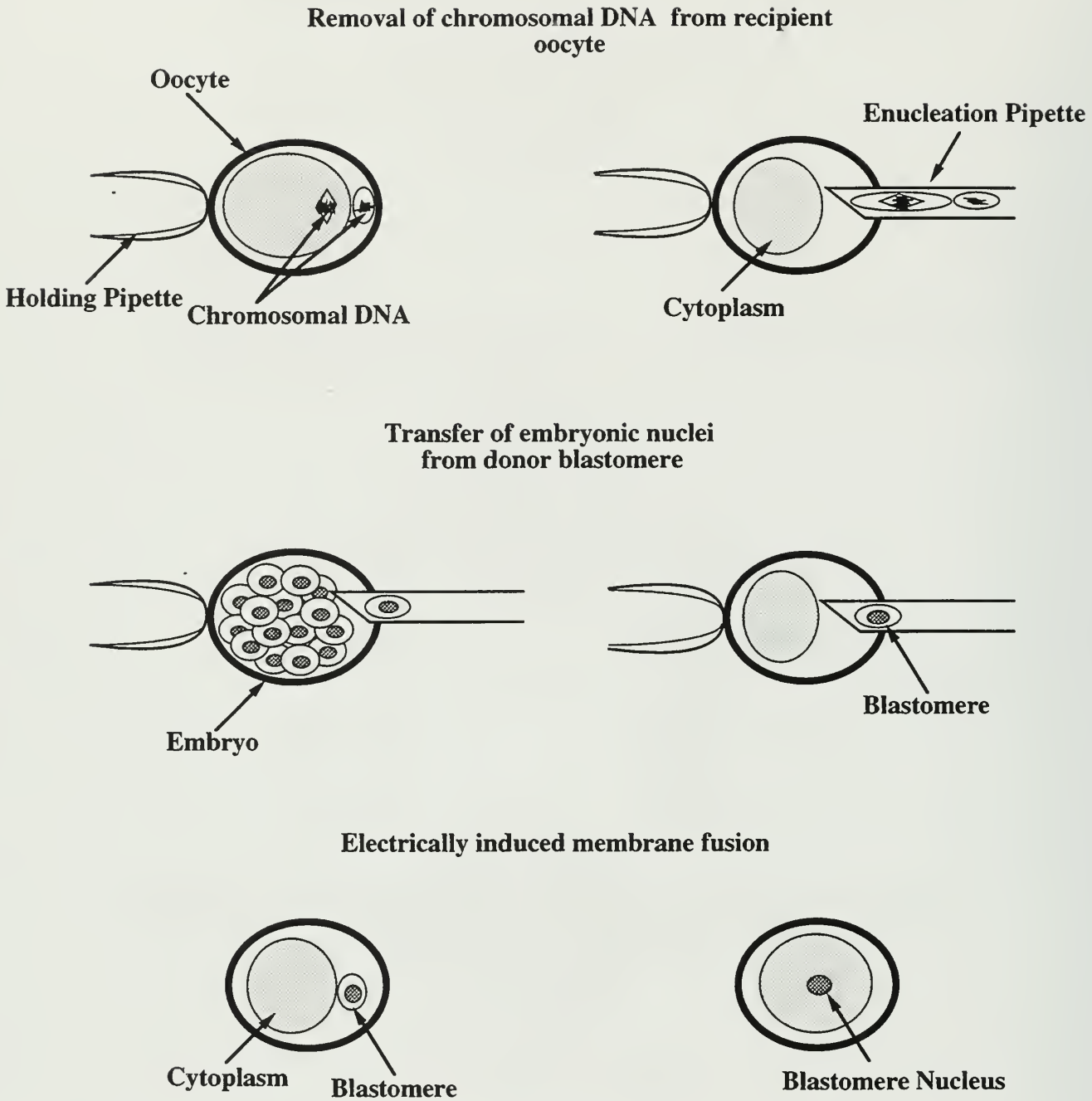

Figure 4: A schematic diagram of cloning by nuclear transfer. Initially, chromosomal DNA is removed from the recipient oocyte (TOP). Next, a blastomere from the donor embryo is transferred to the enucleated recipient oocyte (MIDDLE). Finally, an electrical pulse is generated which promotes fusion of the blastomere and oocyte membranes which transfers the nucleus into the oocyte cytoplasm to initiate embryonic development (BOTTOM). The newly constructed embryo is usually cultured in vitro before transfer to a suitably prepared recipient.

PHYSIOLOGICAL ASPECTS OF THE PRODUCTION OF POLLUTANTS AND MALODOROUS COMPOUNDS BY PIGS

Roderick I. Mackie

Introduction

Animal production results in the conversion of feeds into valuable products such as meat, milk, eggs and wool as well as into unavoidable and less desirable waste products. Animal wastes (feces, urine, respiration and fermentation gases) are excreted in solid, liquid or gaseous form. Respiration and fermentation gases are lost to the environment soon after being produced by the animal. After excretion, solid and liquid animal waste is subjected to (mainly anaerobic) microbial conversions which convert organic substrates into microbial biomass and soluble and gaseous end-products. Intensification of animal numbers and increasing urbanization has resulted in considerable attention to malodorous gases produced from animal wastes. In recent years, attention has also shifted to their impact on the environment and their effects on acid deposition, destruction of the ozone layer and greenhouse effects. Excessive levels of malodorous compounds in the environment may result from high concentrations of animals in confined areas, from less efficient feeding, inadequate storage or application of animal wastes as fertilizer or a combination of these. This paper summarizes knowledge concerning the sources of these malodorous compounds and possible ways of reducing or controlling them.

Sources of Gaseous Pollutants from Farm Animals

Although most of the gases resulting from animal production are not a direct hazard to animal or human health, their smell may be obnoxious which makes them undesirable. Gases produced by farm animals can be divided into three groups namely methane, ammonia and other nitrogenous gases and volatile (mal)odor compounds.

Methane Production in Farm Animals

Anaerobic microbial fermentation contributes substantially to digestion in farm animals, particularly the foregut of ruminants (cattle and sheep) and to a lesser extent the hindgut of monogastric animals (swine and poultry). Organic matter in feed, particularly structural carbohydrates, are fermented to volatile fatty acids (acetic, propionic and butyric acids), microbial

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biomass, fermentation gases (CO_2, CH_4) and heat. This process requires an electron sink which is provided by CO_2 reduction resulting in CH_4 formation:

$$CO_2 + 8[H] \rightarrow 4H_2O$$

The CH_4 and CO_2 are removed from the rumen by eructation and respiration and result in a loss of energy (5-10% GE).

Although CH_4 is odorless it is now clear that it contributes significantly to the greenhouse effect. Farm animals contribute about 20% of worldwide CH_4 production and are thought to be responsible, especially ruminant animals, for a significant part of the increase over the last century.

Production of NH_3 and Other Nitrogenous Gases

Farm animals consume considerable amounts of protein and other nitrogen-containing compounds with their feed. Part of the protein is deposited in the body or excreted in milk, but a large part is lost in feces and urine.

Table 1. Fate of nitrogen consumed in feed by different categories of livestock

Livestock category	Feed protein (g/kg DM)	Body (%)	Milk (%)	Feces (%)	Urine (5%)
Lactating cow					
grazing	250	2	17	25	56
stall fed	175	2	25	34	39
Beef cattle	150	22	-	30	48
Veal cattle	180	54	-	5	41
Lactating sow	160	5	20	20	55
Piglet	184	40	-	10	50
Growing pig	170	32	-	15	53
Laying hen	170	32	-	12	56
Broiler	217	42	-	10	48

Source: Tamminga (1992)

Fecal N may be partly excreted as NH_3 while N in urine is mainly excreted as urea in cattle, sheep and swine and as uric acid in poultry. Other N-containing compounds excreted in urine are allantoin, hippuric acid and creatinine.

After excretion, feces and urine normally become mixed and, due to the presence of large numbers of microbes, degradation of N-containing compounds occurs. An important end-product of this degradation is NH_3, which during storage or after application to the soil as fertilizer can be converted to nitrate or N_2. Side reactions can result in the production of nitrogen oxides (N_2O, NO and NO_2) which escape into the environment. These are believed to contribute to destruction of the ozone layer. At high levels they can be poisonous and threshold limit values (TLV) for humans are 25, 25 and 5 ppm for NH_3, NO and NO_2 respectively for an 8 hr exposure. Farm animals are exposed to these gases almost continuously and therefore levels of 2-10 ppm NH_3 are considered safe (Tamminga and Verstegen, 1992).

Volatile Noxious Odors

About 60 volatile components have been identified in animal waste (Spoelstra, 1978) of which a dozen are considered important contributors to malodor. Noxious odors escaping from animal manure can be classified as volatile carboxylic acids (acetic, butyric, propionic and branched-chain fatty acids), indoles (skatole and indole) and phenols (cresol, 4-ethylphenol, phenol) ammonia and volatile amines (NH_3, putrescine, cadaverine) and sulfur containing compounds (H_2S, dimethyl sulfide, methyl mercaptan, ethyl mercaptan) (Mackie, 1995). The odor threshold value (OTV) and the threshold limit value (TLV) of these compounds in air are presented in Table 2. Generally, TLV's are at least a factor of 500 higher than OTV's and thus, these odors are detected long before their concentrations become a health risk. "Normal" values in farm buildings (pig houses) are usually far below the TLV, except NH_3 and H_2S, which can reach dangerous levels.

Table 2. Odor threshold values (OTV's) and lowest toxic values (LTV's) of noxious compounds found in confinement houses

Compound	OTV (ppb)	LTV (ppb)
Ammonia	4,700	25,000
Acetic acid	1,000	10,000
Phenol	5	5,000
Methyl mercaptan	2	500
Butyric acid	1	-
p-Cresol	1	5,000
Ethyl mercaptan	1	500
Dimethyl sulfide	1	1,000
Hydrogen sulfide	0.5	10,000

Source: Tamminga (1992)

The lowest OTV's are for sulfur-containing compounds which are expected to originate partly from degradation of S-containing amino acids. Part of the H_2S is derived from reduction of inorganic sulfate rather than S-containing amino acids. Also, H_2S is highly reactive being rapidly oxidized. Most of the other odors also originate from the anaerobic degradation of protein through deamination, dehydroxylation and decarboxylation of amino acids. An important reason for this degradation is that animal waste contains a surplus of N-containing compounds (0.10-0.16 ratio of N to non-N compounds) which is much higher than an optimal ratio (0.03) required for microbial growth.

Measures to Reduce Gaseous Pollutants from Animal Wastes

Gaseous losses from animal enterprises originate partly from animals and partly after microbial conversions in stored waste. All animal classes make a significant contribution of loss of NH_3. Freshly voided feces and urine contains little ammonia, but it is produced rapidly during storage.

Methods of reducing losses in NH_3 include: i) reducing the excretion of compounds from which NH_3 is formed; ii) preventing the conversion of urea into NH_3; iii) preventing the escape of NH_3 from stored animal waste. These strategies have been discussed by Tamminga (1992).

Noxious odors are largely end-products protein degradation either excreted in feces or from lysis of microbes which grow during the early stages of waste storage. A positive relationship has been found between excretion of NH_3 and excretion of malodor compounds which suggests that NH_3 can be used as a marker of malodor excretion because of difficulties in measuring these compounds. Various ways have been tested to control the escape of noxious odors. These include the use of biofilters, acidification and finally fermentation.

Indole Compounds and Boar Taint

Originally boar taint was ascribed to the presence of the male sex hormone androstenone in entire male pigs. More recently another group of compounds, the indoles, have been implicated as major factors in boar taint. The indole compounds (skatole and indole) are formed in the large intestine (and feces) by bacterial degradation of tryptophan. Although little in known about the production and metabolism of skatole and indole, it is apparent that absorption of skatole is highly efficient since skatole infused into the hindgut resulted in less than 4% of infused skatole being recovered in feces. Within the body absorbed skatole accumulates in adipose tissue. In the pig, only a relatively small proportion of dietary amino acids reach the hindgut and may explain why experimental addition of tryptophan has negligible effects on skatole levels in adipose tissue. Changes in dietary protein content have been reported to alter skatole concentration in adipose tissue, although this appears to be an indirect rather than direct effect (Moss et al. 1992). Addition on skatole in the diet results in increases in skatole concentration in adipose tissue. Dietary components which indirectly affect skatole production through the gut-microbiota include dietary fiber and antibiotics. Although a sex/feeding interaction has been observed, with boars having significantly higher concentrations of skatole in adipose tissue compared to castrates and gilts, it is unlikely that gut-microbiota differs between sexes. It seems likely, however, that sex

hormones such as androstenone facilitate passage of lipophilic substances across biological membranes. Behavioral observations of rooting behavior in boars and ingestion of feces were also unable to satisfactorily explain sex differences in skatole levels in adipose tissue (Claus et al. 1994). Thus, in order to control skatole levels in pig back fat, considerable research effort directed at understanding hormonal and non-hormonal mechanisms is essential.

Conclusion

Malodor emanating from swine production facilities and swine manure is a major problem for the pig industry in the USA. Poor odor prevention and control is directly related to a lack of knowledge on the fundamental nature of odor and its production by pigs. High levels of odor components are also reported to reduce growth performance, influence carcass quality and increase susceptibility to disease in pigs. Thus, a sustained research effort which combines modern analytical techniques and the latest sensory technology to determine the fundamental animal and microbial factors involved in the production of pollutants and malodorous compounds is critical.

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STRATEGIES IN THE PRODUCTION OF "USER-FRIENDLY" PORK

EDWIN T. MORAN, JR.[1]

Introduction

A basic tenant of business is "always know what your competition is doing." Poultry is the primary competitor of pork for the comsumer's meat dollar. Both meat sources are remarkably similar in terms of commercial genetic concerns, basic grow-out facility, feedstuffs employed, nutrient requirements, processing yields, and presence of white and dark meats. Yet, poultry has gained substantial market share during the past decade whereas, pork consumption per capita has changed little.

The purpose of this communication is convey a competitor's perspective. Central to relating production strategy from this view is an understanding of the term "user-friendly." It's purpose is emphasize that each meat product or market line has one or more economically critical features central to its use. Such features may be measured in terms of reproductive rate, fatness, fleshing, weight, color, etc., and values critical to a primary facet determining disappearance for one product may have little bearing on another.

The Growth Curve and Meat

All meat animals have similar carcass characteristics as they progress through each stage of development. Essentially, infant growth is slow and represents a transition of an embryonic body to one competent at self-sufficiency. Subsequent juvenile development is a rapid escalation of all features to approach adult stature followed by the inflection point and initiation of alterations for reproduction. Characteristics of the carcass for food purposes are modified at each stage, and animals for meat are seldom marketed too far into adolescent development.

Bone, meat, and fat depots denominate the body's view as a food source. Skeletal development during infancy is heavily committed to calcification and structural stabilization of the cartilage frame that was embryologically established. Rapid expansion of this frame occurs through juvenile growth then it progressively decreases after the inflexion point.

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Muscle accrual during infant growth rapidly "fleshes" the skeleton to enable mobility and all activities necessary for independent living. Muscle gained during juvenile growth increases proportionately with bone throughout the body; whereas, preadolescent development focuses on a few muscles that are specialized to accommodate adult need. Muscles directly involved in reproduction become exaggerated. Muscles secondarily also involved are likely to grow substantially, and these are used extensively for food. The breast of fowl and loin with mammals have economic importance in this respect.

Depot fat is strategically located throughout the body, and their growth and emphasis changes with stage of development similar to muscle. The smallest yet most important in terms of food are the intermuscular depots which come into prominence during preadolescent growth. These depots are not trimmed because their presence is considered valuable to sensory value. Correlation between intermuscular fat and sensory improvement is poor to suggest that their presence is more a hallmark for other changes than direct involvement.

Age at which events in the growth curve occur as well as either accentuation or diminution of muscle and fat can be genetically altered by selection. Measurements employed and stage of development when taken will determine the tissues likely to be influenced and extent of response. Selection pressure to increase high value meats and reducing depot fat is often unfavorable to reproductive traits; thus, carcass advantages in this respect must be economically recovered in one manner or another to offset reproductive losses.

Strategy and Objective

The most crucial aspects of each product line in the sequence of events from parent stock to consumer dictates strategy. Genetics, nutrition, and management represent the strategic means to create a user-friendly situation. Integrated operations are particularly favorable in synchronizing strategy with objective, and the poultry industry has been successful with each of their type markets. A cursory view of poultry markets, features critical to each, and strategies employed provide examples where similar approaches might be applied to the pork industry.

Whole carcasses were the original market, and grading "A" was the primary objective. Physical defects are an extensive problem which become greater as carcass weight (bird age) increases. Strain-cross selection is important because major differences in the nature of defects and their incidence can occur among sources. Marketing close to the inflection point improves fleshing and finish. Inordinate nutrition is unnecessary; however, reduced bird density decreases "contact" defects.

Cut-up carcass use came into prominence when fast-food outlets appeared. Precooked pieces did not compete with the whole carcass market but extended per capita consumption. The most critical aspect of this product was necessity of a narrow weight range to accommodate established cooking procedures. These ranges invariably necessitate using birds at the juvenile

stage of development, and heavily fleshed strains would not readily convey advantage at light weights. Sex-separate rearing enables greater proportions of any one flock to fall within the desired weight range.

Eight and nine piece cuts are specific to deep-fat frying. Loss of body fat into cooking fat leads to its deterioration as the amount leached and its degree of unsaturation increase. This concern is likely to be addressed in the near future with the use of low fat strains and nutritional regiments that minimize depot accrual and degree of unsaturation.

Further-processing was initiated with the need to obtain breast "nuggets" for the fast-food trade. This departure from classical carcass use led to breast fillets, tenders, hot wings, and a multitude of other secondary products. For the most part, these new items did not compete with pre-existing poultry meats as much as provide diversification that was in harmony with the public "need."

Unquestionably, breast meat is the most economically sensitive part, and the use of high yielding strains becomes a necessity. Full realization of potential requires strict attention to protein nutrition and marketing past the inflexion point. All these factors increase production cost; but, monetary returns more than compensate the difference under these value-added circumstances.

Rotisserie outlets have recently extended whole carcass use. This carcass line does not compete with those at the super market because of the special type cooking and convenience access. Appearance is very critical, and strains exhibiting exceptional fleshing and finish together with high performance feed are necessary. The added cost of genetics and nutrition is small compared to value of final product.

Total quality management (TQM) is another way of viewing user-friendly strategy. Crucial aspects in the overall scheme of production are the focus of attention. Whole carcass, cut-up, and further-processing markets differ in their crucial aspects, in turn, imposition of strain and sex, age to market, nutritional concerns in formulation, and flock management can vary in strategy for optimization. Integrated operations facilitate full exploitation of strategy.

Strategy for Pork Production

Increased pork must relate to public "need." Escalation of poultry consumption essentially resulted from development of products beyond traditional. Whole carcass used has not changed per capita since it plateau 20-30 years ago until recently with the appearance of rotisserie outlets. Cut-up and further-processed use has grown because product array and timing were synchronized to perception of health benefits and need for convenience.

Integrated operations in the production of pork represent a departure from the traditional grower-packer scheme. Pork quality has increased substantially, but the whole orientation is for traditional markets served by the packer. If growth of market share is to be realized, then

"new" products must complement those existing and agree with today's lifestyles. Integrationed production complexes that focus on user-friendly concerns would be particularly appropriate to "new" markets.

An example of a "new" product line remote from the classical meats, yet is clearly "pork" involves the recent and highly successful rotisserie outlets. These outlets have expanded their menu to include meats other than chicken, and the weaner pig seems particularly appropriate for this purpose. Certainly, the image is familiar to the public and unavailable otherwise. A complex devoted to this end would probably have herd fecundity as a dominant concern while associated nutrition and processing are also uniquely important. Possible? - An entertaining thought at the least.

IMMUNOMODULATION OF GROWTH IN SWINE

BRIAN N. FINCK AND RODNEY W. JOHNSON

Introduction

Even though disease and animal growth have long been two of the most important issues in swine research, only recently have we begun to understand why sick or immune challenged pigs grow slowly. Disruption of an animal's internal milieu by infection or injury threaten its integrity and require immunological, behavioral and physiological responses so that a relative homeostatic state may be achieved. These responses may be subtle, as is probably the case for swine with a subclinical, chronic, low-grade infection. Other instances, however, require a more extensive response. In any case, there is a deliberate shift in the partitioning of dietary nutrients. This complex, known as immunological stress, suppresses voluntary food intake and alters the partitioning of nutrients away from growth and skeletal muscle accretion in favor of metabolic processes that support the immune response (see Klasing and Johnstone, 1991). This shift in the balance between anabolic and catabolic processes forms the basis for impaired growth and feed utilization in animals subjected to infectious and noninfectious agents. The purpose of this brief article is to discuss the mechanisms of immunological stress in swine.

Immunological Stress and Cytokines

Several years ago, Kirk Klasing (1988) proposed that cytokines released during the immune response are major mediators of intermediary metabolism in immunologically stressed animals. This hypothesis was based on a series of experiments in chicks which demonstrated that a variety of inflammatory agents reduced food intake and efficiency of gain, increased body temperature, increased plasma corticosterone and altered the distribution of zinc, iron and copper (Klasing, 1984; Klasing et al., 1987; Klasing and Barnes, 1988). More than 70% of the reduction in weight gain was due directly to a reduction in voluntary food intake. After Klasing's group used cell-free supernatant from stimulated macrophages to induce the same responses (Klasing et al., 1988), it was obvious that an immunogenic component, rather than a pathogenic component was responsible for the anorectic and metabolic effects. These data confirmed previous reports in rats and mice (Beutler and Cerami, 1988), and strongly implicated a group of proteins released by mononuclear myeloid cells (e.g., macrophages) called cytokines.

Cytokines were first described as soluble molecules that mediate interactions between cells participating in the immune response. As shown in Figure 1, the macrophage releases at

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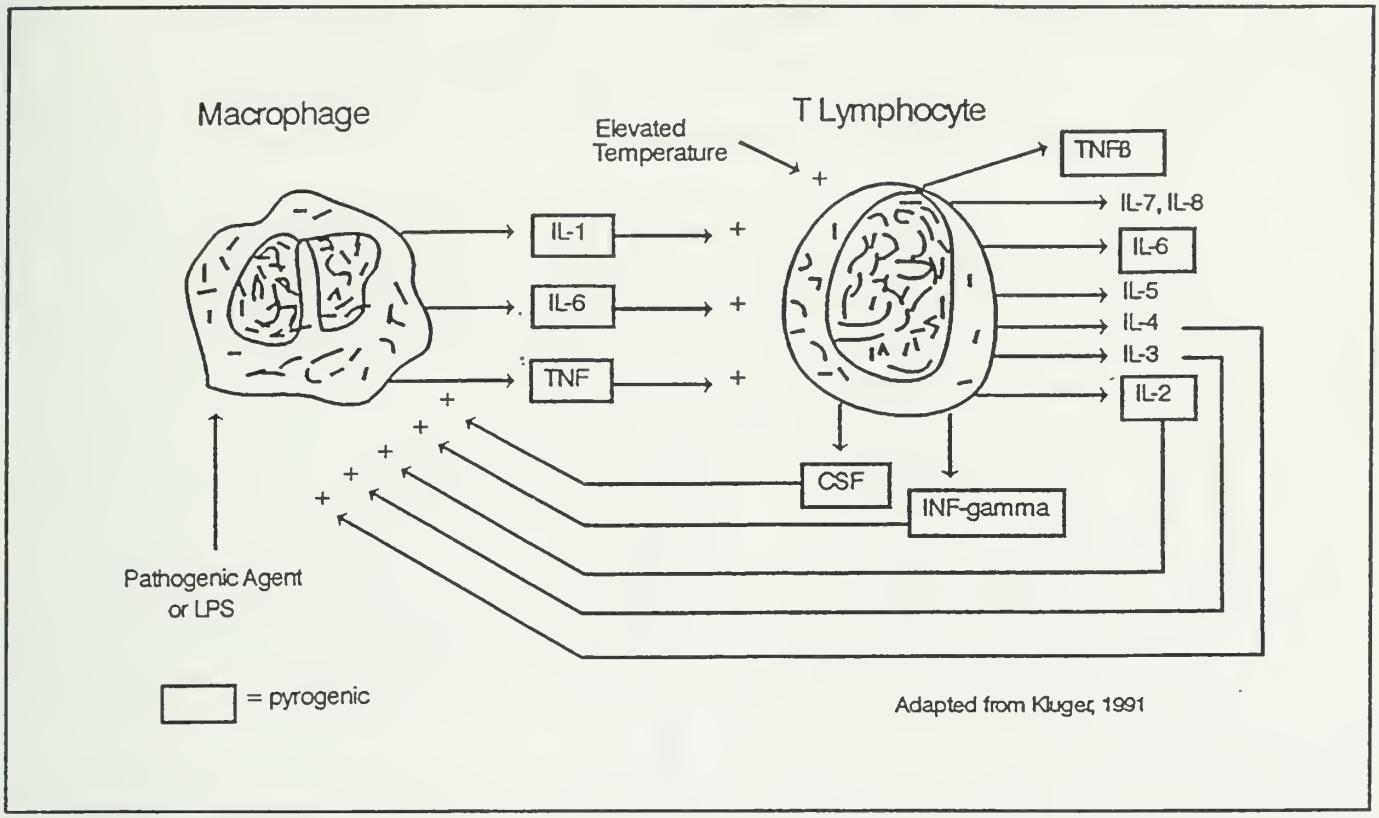
least three major cytokines when exposed to inflammatory agents. These include interleukin-1 (IL-1), interleukin-6 (IL-6) and tumor necrosis factor alpha (TNFα). These molecules act locally to amplify the cellular immune response, but also act on a number of behavioral, physiological, and neuroendocrine targets. There is now considerable evidence suggesting that the behavioral and physiological symptoms of sickness are integral components of the acute-phase response and are important for maintaining homeostasis during infection (Hart, 1988; Kent et al., 1992). Thus, cytokines are important messengers used by the immune system to inform the rest of the body that an infection has been established.



Reduced food intake, inactivity, fever and sleep are behavioral states observed in animals with an acute bacterial or viral infection. In addition, a number of neuroendocrine and metabolic alterations are apparent in sick animals including decreased growth hormone secretion, increased secretion of glucocorticoids and increased hepatic synthesis of acute-phase proteins. These responses are non-specific to the invading pathogen and are also attributed to cytokines. Because porcine macrophages produce the same array of cytokines (Murtaugh, 1994; Zhou et al., 1994), the emerging view is that the reduction in food intake, lean muscle accretion, and growth in immunologically stressed pigs is the result of increased cytokine activity. However, this important point has not been directly tested in any domestic animal species.

Our understanding of the anorectic and metabolic effects of cytokines in swine (and most domestic animals) has severely lagged. This is at least partially due to the unavailability of recombinant porcine cytokines (Murtaugh, 1994) and the inability to accurately measure cytokines in biological fluids. A typical approach to studying immunological stress in swine has been to administer lipopolysaccharide (LPS), or endotoxin. Lipopolysaccharide is a

molecule found in the membrane of all gram negative bacteria. When administered i.p. to swine it induces symptoms of acute bacterial infection including anorexia, hypersomnia and fever (Johnson and von Borell, 1994). The effects of LPS are attributed to its ability to stimulate macrophages to synthesize and secrete proinflammatory cytokines, primarily IL-1, IL-6 and TNFα (Figure 1).

There are a number of practical considerations for better understanding the role of proinflammatory cytokines in growth of swine. This point is emphasized in Figure 2. There are at least two widely used practices in swine production for reducing exposure to infectious and noninfectious agents. First, since the initial observation some 40 years ago that antibiotics improve animal growth and efficiency (Stokstad et al., 1949), antibiotics have

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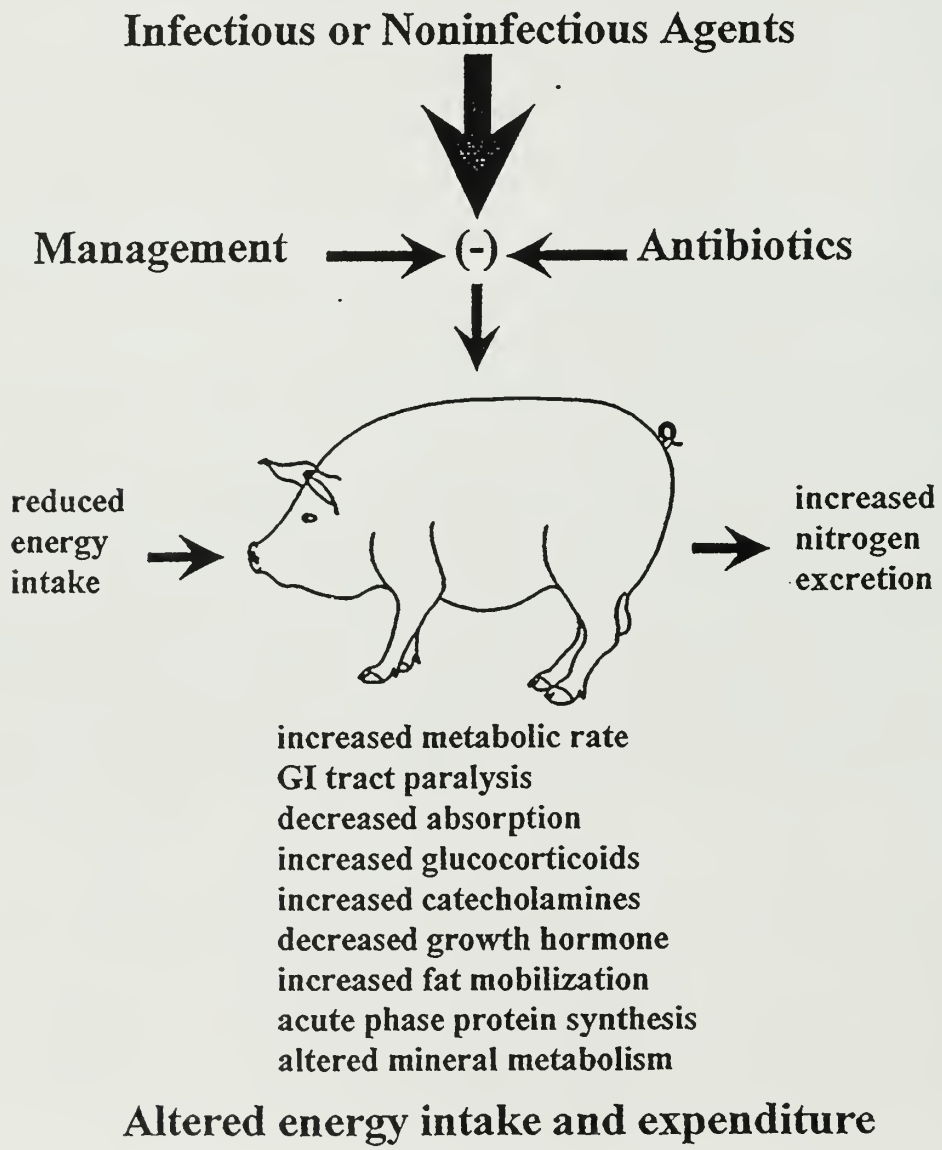
Figure 1. Good management minimizes the impact of pathogens on swine growth but is not entirely successful. This diagram depicts immunological stress and its effects on factors likely to impact growth and efficiency of swine.



been used as feed additives in subtherapeutic amounts to reduce immunological stress (Cromwell, 1991; Roura et al., 1992). Second, it is well known that pigs kept under management schemes that presumably provide less immunological stress (e.g., Medicated Early Weaning and all-in, all-out) typically consume more feed, grow faster and retain more nitrogen for proteineous tissue growth (e.g., Williams et al. 1993a,b). Failure to control or regulate exposure to infectious and noninfectious agents can have dramatic metabolic consequences as shown in Figure 2. It should be noted that this complex is well-defined in laboratory animals, but not swine. Nonetheless, these effects have been tentatively related to cytokines because anorexia and metabolic inefficiencies are induced in rodents by administering recombinant cytokines like IL-1, IL-6 and TNFα (Kelley et al., 1994). An understanding of the effects of cytokines is therefore a prerequisite to understanding and ultimately improving the growth and efficiency of immunologically stressed swine.

Cytokines Modulate Intermediary Metabolism

Beutler and Cerami (1988) were first to suggest that in response to antigenic stimuli, a variety of cells, including activated macrophages and lymphocytes, secrete cytokines which are responsible for alterations of the host's metabolism. Three of these cytokines, IL-1, IL-6 and TNFα, have profound metabolic effects. When injected systemically, they induce behavioral, metabolic and neuroendocrine alterations similar to those seen in chronic infections, including depression of food intake, diarrhea, hypertriglyceridemia, hypoferremia, hypozincemia, hypercuppremia and protein wasting. Based on studies in lab animals, it is clear that increased secretion of TNFα is likely to have profound effects on the growth and efficiency of animals. A partial list concerning the role of TNFα in intermediary metabolism, as well as comprehensive reviews on each subject, is provided in Table 1.

A salient feature that characterizes cytokines is their redundancy, as defined by the ability of different cytokines to exhibit the same functions. The major proinflammatory cytokines that share considerable biologic properties and are released by activated macrophages (as well as other cell types) are IL-1, TNFα and IL-6 (extensively reviewed by Dinarello, 1991). All three molecules induce synthesis of hepatic acute-phase proteins, activate both T and B cells, stimulate the hypothalamic pituitary adrenal axis, and induce fever. In addition, both IL-1 and TNFα induce anorexia, hypersomnia, and depress social behavior. However, despite the pleiotropic and redundant nature of cytokines, it is clear that certain cytokines are better than others at inducing certain responses. For example, IL-1 is more potent than TNFα for reducing nutrient intake (Plata-Salamán et al., 1988), altering glucose metabolism (Memon et al., 1994), and inducing certain sickness-related behaviors (Bluthé et al., 1994a). IL-1, however, does not induce lipolysis, and hence its effects on serum triglyceride levels are secondary to enhanced fatty acid synthesis and very low-density lipoprotein secretion which are primary functions of TNFα (Memon et al., 1994). Whereas IL-1, TNFα and IL-6 have been shown to stimulate corticotropin-releasing hormone neurons in the hypothalamus (Rivier et al., 1989; Navarra et al., 1991; Kakucska et al., 1993; Perlstein et al, 1993), there are new data to suggest that the cytokine involved is dependent upon the level of immunological stress (Ebisui et al., 1994). Furthermore, whereas the muscle proteolysis caused by TNFα involves glucocorticoids since some components are inhibited by surgical or chemical adrenalectomy, the IL-1-induced proteolysis does not (Zamir et al., 1992; Zamir et al.,

1993). Therefore, it is extremely likely that the individual properties of the various cytokines converge to formulate the animal's overall metabolic state.

Table 1. Partial list of metabolic effects of recombinant TNFα

Metabolic Target and Effect	Reference Article
Central Nervous System	
Fever	Kluger, 1991; Moltz, 1993
Anorexia	Kent et al., 1992;
HPA Axis Activation	Blalock, 1994a,b; Tilders et al., 1994
Lipid Metabolism	
Lipolysis	Beutler & Cerami, 1989
de novo fatty acid synthesis	Memon et al., 1994
Inhibition of lipoprotein lipase activity	Memon et al., 1994
Decreased uptake of blood triglycerides	Grunfeld & Palladino, 1990
Increased hepatic VLDL secretion	Feingold & Grunfeld, 1987
Hypertriglyceridemia	Grunfeld & Feingold, 1991
Carbohydrate Metabolism (biphasic response)	
Phase I. Hyperglycemia	
Gluconeogenesis	Andus et al., 1991; Memon et al., 1994
Glycogenolysis	Andus et al., 1991; Memon et al., 1994
Phase II. Hypoglycemia	
Decreased PEPCK activity	Hill & McCallum, 1992
Increased glucose oxidation	Spitzer et al., 1989
Increased glucose utilization	Spitzer et al., 1989; Andus et al., 1991
Protein Metabolism	
Breakdown of skeletal muscle	Klasing, 1988
Increased hepatic amino acid uptake	Andus et al., 1991
Acute-phase protein synthesis	Andus et al., 1991
Mineral Metabolism	
Hypozincemia	Klasing, 1988; Andus et al., 1991
Hypoferremia	Klasing, 1988
Hypercupremia	Klasing, 1988
Hypercalcemia	Andus et al., 1991

Although information concerning the metabolic effects of cytokines in pigs is scant, a wasting syndrome has been described in pigs (Kyriakis and Andersson, 1989; Morrow-Tesch and Andersson, 1994). In humans and laboratory animals wasting, or cachexia, has been attributed to increased secretion of TNFα. Wasting pigs express a chronic anorexia, a reduced weight gain and a number of metabolic disturbances including hypozincemia and decreased plasma alkaline phosphatase (Kyriakis and Andersson, 1989). Jewell et al. (1988) demonstrated that human TNFα (i.e., cachectin) and sera from pigs infected with *Sarcocytis*

suicanis showed lipolytic activity on adipocytes *in vitro*. Furthermore, our own lab recently reported that central injection (i.e., into the lateral ventricle of the brain) of recombinant porcine TNFα reduces food intake, increases cortisol secretion, and elicits behavioral symptoms in pigs reminiscent of sickness (Warren et al., 1994; 1995). Collectively, these data suggest that TNFα may be important for modulating metabolism in immunologically stressed pigs.

Conclusion

It is now clear that cytokines inextricably link the immune system to other physiological systems. Only recently, however, have we begun to understand the implications of increased cytokine production for animal growth. The cytokines released by activated macrophages orchestrate the behavioral, metabolic and neuroendocrine responses that culminate in slower, less efficient growth. A better understanding of the biological actions of cytokines is needed before the immune system's contribution to pig growth can be fully appreciated.

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GASTROINTESTINAL HEALTH AND GROWTH OF YOUNG PIGLETS

H. REX GASKINS

Introduction

Major productive losses in the swine industry are encountered from birth to weaning. Although causative factors likely result from numerous interactions between the piglet and its new environment, low immunocompetency at birth resulting in heightened susceptibility to intestinal pathogens is certainly a major reason underlying these production losses. Several developmental aspects of the pig's immune system contribute to low immunocompetency at birth which have a significant impact on the survival of newborn piglets. For example, a specialized epitheliochorial placentation does not allow the passage of maternal antibodies (immunoglobulins, Ig) to the fetus and thus the piglet is born without the safeguard of passive immune protection (see review by Holland, 1990). The immune system of the newborn piglet is also anatomically and functionally immature, making survival dependent on passive transfer of maternal antibodies in colostrum and milk (Stokes and Bourne, 1989). Thus, newborn pigs are especially vulnerable to pathogenic challenge during the period in which antibody levels have declined in milk and before active immune mechanisms are developed.

Our research program is focused on defining host and microbe defense mechanisms operative in the pig intestine. Understanding the temporal patterns of intestinal immune system development and determining the degree to which intestinal immunity can be enhanced in newborn pigs is of particular interest. A general overview of intestinal defense mechanisms is provided below and followed by a discussion of what is understood currently about the development of immunity in the pig. Throughout, target mechanisms are identified that might lead to strategies enabling an early boost in active immunity.

Gastrointestinal Defense Mechanisms

The gastrointestinal tract provides an extensive surface area in which intimate contact takes place between the host organism and a wide variety of dietary substances and their breakdown products as well as microorganisms, parasites, and exogenous toxins. Accordingly, the intestine must permit the exchange of dietary substances between the gut lumen and the systemic circulation, but, at the same time, prevent penetration of pathogenic agents.

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Thus, it is not surprising that a dense array of mucosal defense mechanisms are operative in the intestine. These intestinal defense mechanisms can be classified generally as being either nonspecific or specific in nature.

Nonspecific Defense Mechanisms

The stomach, where the extreme acidity limits the number of viable microbes that gain access to the small intestine, represents one of the most important nonspecific defense mechanisms. Those microbes that survive the acid conditions in the stomach are rescued by the more alkaline conditions of the small intestine which are necessary for nutrient absorption. Being more alkaline, the conditions found in the small intestine are more favorable for microbial growth and thus the potential for close contact and attachment of microbes to the mucosal epithelium is increased. However, the host compensates through additional nonspecific defense mechanisms and by boosting its immune defenses in the small intestine.

Nonspecific defense mechanisms in the small intestine include biliary secretions to which some microbes are sensitive, and pancreatic secretions that contain proteolytic enzymes which can degrade bacterial cell walls. The epithelium itself serves as a barrier with tight junctions between each of the enterocytes forming an epithelial monolayer and thereby preventing the passage of large molecules. The rapid turnover of enterocytes every 3 to 6 days also minimizes the opportunity for epithelial attachment of potentially pathogenic microbes. Intestinal motility and forward propulsion also prevents adherence of microbes to the epithelium in the small intestine. Mucus, secreted by a specialized type of enterocyte (goblet cells), acts as a lubricant to protect the delicate epithelial surface from gastric acid secretions and prevents physical attachment of microbes to the intestinal epithelium.

The conditions found in the large intestine, including a near-neutral pH, anaerobiosis, and diminished motility, favors the growth of an abundant normal microbiota. In addition to serving as an important source of nutrition for the host, these indigenous gut bacteria are critically important for the development and maintenance of healthy gastrointestinal function. Perhaps the most important contribution of the normal microbiota to the host is its ability to inhibit the colonization of invading microorganisms in the intestine (Hentges, 1983). The proposed mechanisms of microbial interference afforded by the resident microbiota include an inhospitable pH, competition for nutrients (Bartlett, 1979) and attachment sites on the intestinal epithelium (Brock, 1966), and the local production of antibiotics known as bacteriocins (Savage, 1972). There is increasing evidence that normal gut bacteria also enhance host immunity by stimulating specific immune mechanisms at the mucosal and systemic level (Gaskins, 1996).

Specific Defense Mechanisms

Approximately one-quarter of the intestinal mucosa is comprised of lymphoid tissue and greater than seventy percent of all immune cells, including those found in bone marrow, thymus, spleen, and lymph nodes, are located within the intestine (Kagnoff 1987; Hinterleitner and Powell 1991; Kagnoff 1993; Kraehenbuhl and Neutra 1992). Cellular

components of the intestinal immune system include dispersed or nonaggregated cells (lamina propria leukocytes and intraepithelial lymphocytes [IEL]), as well as highly organized lymphoid follicles such as the Peyer's patches where secretory Ig A^+ B lymphocytes are generated.

Secretory IgA

The best described immunologic barrier in the intestine is secretory IgA. These immunoglobulin molecules are synthesized by B lymphocytes that are first exposed to antigens in Peyer's patches, a collection of organized germinal centers found in the intestine (Mestecky 1987; Kraehenbuhl and Neutra 1992; Kagnoff 1993). Luminal antigens are transported through specialized epithelial cells (membranous or M cells) overlying Peyer's patches, into an interfollicular area where they are presented by resident antigen presenting cells to helper T (T_H) lymphocytes. The T_H cells, in turn, secrete cytokines that stimulate B lymphocytes to undergo immunoglobulin class-specific switching resulting in B lymphocytes that produce a single class of antibody. For reasons still unknown, the microenvironment in Peyer's patches favors class-specific switching to an IgA^+ phenotype (Kagnoff 1993). After leaving Peyer's patches and passing through the systemic circulation, IgA^+ B lymphocytes migrate back to the lamina propria (more prominent in the crypt than villus region) where they differentiate into plasma cells capable of secreting large amounts of antibody. Upon reintroduction of the antigen, plasma cells secrete antigen-specific IgA which is then transported back toward the intestinal lumen across the epithelium by a specialized epithelial receptor (secretory component), and released onto the mucosal surface (Mostov, 1994). Mucosal IgA antibodies provide protection by preventing adherence of bacteria or toxins to intestinal epithelial cells, by killing pathogens directly, and via antibody-dependent cell-mediated cytotoxicity (Kraehenbuhl and Neutra, 1992; Kagnoff 1993).

The Lamina Propria

The area below the epithelial monolayer and down to the muscularis mucosa, commonly referred to as the lamina propria, contains a large, diffuse population of macrophages, dendritic cells, T lymphocytes, Ig-containing cells (B lymphocytes and plasma cells), mast cells, eosinophils and other granulocytes, as well as biologically-active fibroblasts (Hinterleitner and Powell 1991). This area is also well-vascularized and richly innervated by the enteric nervous system. Through cell-to-cell interactions via intricate signaling networks, the lamina propria plays a vital role in both innate and immunolgic defense mechanisms in the intestine.

As an example of the cellular density of the lamina propria, macrophages, originating from blood monocytes, are present in the noninflammed intestine in numbers of approximately 10^7/g wet weight of tissue (Beeken et al. 1984; Hume and Doe 1988). Lamina propria macrophages play a protective role by phagocytizing and killing microorganisms that have penetrated the mucosal barrier, as well as initiating local immune responses and regulating extracellular matrix formation. These functions are mediated by local release of a large number of signaling molecules, such as cytokines, growth factors, bioactive lipids (prostaglandins, leukotrienes, and platelet activating factor), proteases, phospholipases, and

reactive oxygen species (Nathan 1987).

The lamina propria also contains a large number of mast cells which differ from the classical tissue mast cell in morphological, histochemical and functional characteristics (Saavedra-Delgado et al. 1984; Befus et al. 1988; Schwartz 1994). Mucosal mast cells often reach concentrations of 2×10^4 mast cells/mm^3 of intestinal tissue (Befus et al. 1988). Within the lamina propria there is a close functional and morphological relationship between mast cells and enteric nerve fibers (Saavedra-Delgado et al. 1984; Hinterleitner and Powell 1991). Mast cells are the primary cell type involved in immediate hypersensitivity or allergic reactions and thus of utmost interest when food allergies are considered.

Resident polymorphonuclear granulocytes (eosinophils and neutrophils) present in noninflammed gut may have different properties than their blood-circulating counterparts (Hinterleitner and Powell 1991). The eosinophil is the predominant phagocyte resident in the intestine where it is present in numbers of 1.5×10^6 cells/g wet weight, approximately one log greater than resident neutrophil numbers. The act of phagocytosis or the occupation of surface receptors by chemotactic agents will cause eosinophil and neutrophil degranulation (Sandborg and Smolen 1988). Many of the products released by eosinophils and neutrophils are the same as those released by macrophages. However, even higher concentrations of reactive oxygen metabolites and bioactive lipids (prostaglandins, leukotrienes) are secreted.

In addition to IgA^+ plasma cells and B lymphocytes, a number of T cell subsets and other classes of B lymphocytes are found in significant numbers in the lamina propria. Except for the unique features of secretory IgA, the T and B cells found in the lamina propria contribute to cellular and humoral immunity in the intestine largely through conventional mechanisms (Kraehenbuhl and Neutra 1992; Kagnoff 1993).

Acquisition of Passive Immunity by the Newborn Pig

Specific details of active immunity were reviewed above to emphasize the cellular and molecular complexity of these mechanisms. For pigs, it is clear that these active immune mechanisms are not fully developed at birth. Furthermore, maternal antibodies found in serum are not transferred through the placenta in the pig as they are for most species, but instead are selectively concentrated in colostrum towards the end of gestation (Holland, 1990). Because the functional status of the newborn piglets' immune system is under-developed, colostral antibodies provide the first source of immune protection. Accordingly, immunity in the newborn pig is first limited by the quantity and quality of antibodies in colostrum and by the amount the neonate is able to consume and absorb (Holland, 1990). Moreover, the initial antibody repertoire of the newborn is restricted to those antigens to which the sow has been exposed to and has developed memory B cells (Porter, 1986). The predominant immunoglobulin isotype in colostrum is IgG. Although protection against many systemic pathogenic agents will be provided by maternal IgG, most of the pathogenic agents encountered by the newborn pig are found at mucosal surfaces where IgG antibodies are rarely found and largely ineffective.

Perhaps in response to this limitation, as colostrum formation ends and lactation proceeds, IgG concentrations decrease quickly and IgA becomes the major immunoglobulin isotype in sow milk (Bourne *et al.*, 1978). The switch to a predominance of IgA is a reflection of the mammary gland becoming the major site of synthesis and secretion of milk antibodies (Bourne *et al.*, 1978). Because IgA is, for the most part, resistant to intestinal degradation, high IgA concentrations provide short-term intestinal protection by neutralizing viruses, inhibiting bacterial attachment, and by opsonizing or lysing bacteria (Porter, 1986). Even with a switch to IgA in milk, until active immune mechanisms are established, the newborn is only protected against those antigens to which the sow has previously developed immunity. A better understanding of mechanisms regulating IgA synthesis and secretion in the mammary gland may provide a practical means of assuring that sufficient quantities of specific IgA antibodies are present in milk during the critical period before active immunity is established.

Anatomic alterations occurring in the newborn pig intestine also greatly influence acquisition of maternal antibodies and hence the immune status of individual animals. For example, maximum immunoglobulin absorption in newborn pigs occurs within 4 to 12 h after suckling, and then declines rapidly due to a gradual and progressive process commonly referred to as gut closure (Weström *et al.*, 1985). During this period, colostral immunoglobulins are absorbed across the jejunal epithelium and into lymphatic vessels (Holland, 1990). Absorbed immunoglobulins then enter the circulation (serum) with intestinal lymph through the thoracic duct. Serum antibodies have been detected as early as 3 h after birth (Porter, 1986) and with successful nursing and absorption of colostral immunoglobulins, serum antibody titers of the newborn pig are similar to those of the sow, within 24 h after birth (Holland, 1990). By 48 h after birth gut closure is complete. Although antibody uptake is prevented by gut closure, the process is critical to prevent systemic uptake of other macromolecules which might be pathogenic in nature.

Corresponding to gut closure, immunoglobulin and protein concentrations in colostrum decrease to 50% of prenursing values by 6 h after nursing is initiated. Since average farrowing time in the pig is between 4 to 6 h (Friend *et al.*, 1962; Hendrix *et al.*, 1978), early-born piglets have access to colostrum that is 50% more concentrated in total protein and immunoglobulin content. In the same regard, uncharacterised factors in colostrum are thought to stimulate gut closure (Svendsen *et al.*, 1990). Failure to suckle adequately within the first 24 h of birth could delay gut closure and increase the possibility of pathogenic agents entering the systemic circulation. Thus, there is a short but critical period after birth when the intake of sow colostrum is crucial for the future survival of the pig.

Ontogeny Of Active Immunity in the Pig

Systemic Immunity

Studies addressing development of active immunity in the pig indicate that both reduced numbers and diminished responsiveness of immune effector cells contribute to immunodeficiency in young pigs. For example, the development of B and T lymphocyte

numbers in lymphoid organs of specific-pathogen-free pigs from 2 days before birth until 10 months of age was evaluated recently with immunocytochemical techniques (Bianchi *et al.*, 1992). A detectable number of immature B lymphocytes was present in the spleen, lymph nodes, Peyer's patches (aggregated intestinal lymphoid tissue) and thymus before birth. Just after birth, the number of B lymphocytes increased in an isotype-specific manner with IgM^+ cells increasing first followed by an increase in either IgG^+ or IgA^+ B lymphocytes, depending on the tissue evaluated. In contrast to B lymphocytes, various T-cell subpopulations were well developed before birth in most organs although a postnatal increase in the number of T lymphocytes was observed in spleen and in the lamina propria of the small intestine (Bianchi *et al.*, 1992). Several other studies using similar techniques have verified that although lymphoid organs are generally populated with immune effector cells at birth, there is a numerical increase in phenotypically distinct T and B lymphocyte subsets as well as neutrophils in the developing piglet (Binns, 1973; McCauley and Hartmann, 1984).

Lymphocyte transfer experiments with genetically-defined pigs have demonstrated that, for most tissues, acquisition of tissue-specific homing patterns occurs in the absence of exogenous antigens and is likely one of the first developmental events in the pig. These results further support the notion that immune effector cells are present in lymphoid organs prior to the development of active immunity. Using experimental pig lines that were genetically related, it was possible to show that even at 55 days of gestation radio-labeled postnatal lymphocytes entered Peyer's patches and most lymph nodes at high levels after intravenous injection (Binns and Licence, 1983; Binns and Licence, 1985). Tissue-specific homing patterns were also observed in 72, 93, and 108 day-old fetuses at levels equal to or higher than in postnatal pigs (Binns and Licence, 1985). Thus, the expression of genes encoding molecules that mediate lymphocyte migration to specific tissues appears to develop early in ontogeny, prior to the need for immunocompetent effector cells.

Only a few studies have addressed the functional development of pig lymphocytes. The responsiveness of peripheral blood lymphocytes to T-cell mitogens commonly used in immunological assays has been reported to increase during the first few weeks after birth (Valpotic *et al.*, 1989, Hoskinson *et al.*, 1990). In addition, a recent study directly compared the appearance of certain T lymphocyte cell surface differentiation markers with the ability of lymphocytes isolated from peripheral blood, thymus, and spleen to proliferate in response to T-cell mitogens (Becker and Misfeldt, 1993). Although developmental increases in both the appearance of T-cell differentiation markers and mitogenic responses were noted, a definitive association between the two phenomena was not observed.

Intestinal Immunity

Research efforts to understand the development of active immunity in the piglet intestine have also been very limited. A recent study evaluated developmental aspects of antigen presenting cell functions in the piglet intestine. Lamina propria macrophages, being a predominant type of antigen presenting cell, were distributed equally in villus and crypt regions in low numbers at birth (Vega-López *et al.*, 1993). Soon after birth, macrophages increased in number and began to accumulate in the crypt lamina propria until adult numbers of cells were reached by 5 weeks of age. The number of dendritic cells also increased with

postnatal age; however, these cells accumulated in the villus lamina propria rather than the crypt lamina propria as do macrophages (Stokes *et al.*, 1992). The functional significance of this apparent compartmentalization of antigen presenting cells in the lamina propria is not understood.

Although both T and B lymphocytes are present in the lamina propria at birth in the pig, cell number doubles during the first four weeks after birth (Bianchi *et al.*, 1992; Rothkötter *et al.*, 1991). Parallel with a numerical increase, immature T lymphocytes differentiate with $CD4^+$ and $CD8^+$ T lymphocyte subsets showing distinct patterns of development. Namely, the number of $CD4^+$ T lymphocytes increases dramatically during the first postnatal week, while the number of $CD8^+$ cells is low at birth and increases only moderately by 5 to 7 weeks (Stokes *et al.*, 1992; Rothkötter *et al.*, 1991). In adult pigs $CD8^+$ T lymphocytes predominate in the lamina propria as they do in the blood. In addition, T lymphocyte subsets are segregated with $CD4^+$ cells found predominantly in the center of the villus lamina propria and $CD8^+$ cells near the basement membrane.

The majority of intestinal IEL in humans and in rodent species are T lymphocytes most of which are $CD8^+$ and express the a/b form of the T-cell receptor. However, IEL expressing a more recently described g/d form of the T-cell receptor are also found (Groh *et al.*, 1989; Haas *et al.*, 1993). In the pig many IEL appear during development with most in the young pig being $CD4^-CD8^-$. By 7 weeks of age a significant proportion of $CD8^+$ IEL are found (Stokes *et al.*, 1992). There is at least one report that the ability of IELs to respond to mitogens does not develop until between 9 and 11 weeks of age in the pig (Wilson *et al.*, 1986). As the function of IELs has not been determined for any species, the significance of this developmental lag is unknown. There is much speculation and some evidence that IELs contribute to epithelial integrity by destroying damaged or virus-infected epithelial cells (Kraehenbuhl and Neutra, 1992). Accordingly, the functional development of IEL populations in the pig warrants further investigation.

As discussed above, the best described immunologic barrier in the intestine is secretory IgA which is synthesized by B lymphocytes that are first exposed to antigens in abundant aggregated lymphoid tissue in the intestine called Peyer's patches (Mestecky, 1987; Kagnoff, 1993). In the pig there are approximately 30 discrete Peyer's patches in the jejunum and upper ileum, one long continuous patch in the terminal ileum and approximately 10 irregular spiral Peyer's patches in the colon (Binns, 1982). Although there is a developmental increase in the size of Peyer's patches the number and the position of individual patches remains constant. The composition of lymphocyte subsets within Peyer's patches however does change with age in the pig. For example, IgM^+ B lymphocytes outnumber IgA^+ cells until about 3 weeks of age when IgA^+ cells begin to predominate. Adult numbers of IgA^+ B lymphocytes are reached by 4 weeks of age, while IgM^+ cell numbers continue to increase until 3 to 4 months of age (Brown and Bourne, 1976; Röthkotter, et al., 1991). Increases in T lymphocyte (both $CD4^+$ and $CD8^+$) numbers in Peyer's patches have also been noted for the pig (Pabst *et al.*, 1988; Röthkotter and Pabst, 1989). In summary, depending on the intestinal region in question, active immunity in the pig intestine does not develop until 4 to 7 weeks of age. Significantly, this period of life for the newborn pig corresponds with peak exposure to enteric infectious agents.

Summary and Conclusions

From the discussion above it is obvious that much remains to be understood about developmental events that delay establishment of active immunity in the young pig, and about unique cellular and molecular aspects of the porcine immune system. Our ability to design strategies to boost immunocompetence in the young pig awaits an understanding of not only when but how specific cell types are able to respond to antigenic challenge. Given the degree of cellular interaction required to mount an immune response, a number of specific mechanisms warrant detailed investigation. As enteric pathogens constitute a major economic threat to the swine industry, focusing on developmental aspects of the mucosal immune system might allow more efficient use of limited resources. Considering the extent of neonatal mortality resulting from low immunocompetence in young pigs, intensifying efforts to understand development of active immunity is certain to be profitable.

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HOUSING SYSTEMS TO PROVIDE THE OPTIMUM ENVIRONMENT: ESTABLISHING THE CLIMATIC NEEDS AND RESPONSES OF PIGS

W H CLOSE

The main function of housing is to provide an optimum environment within which animals can achieve high rates of growth and efficiency of feed utilisation, yet live comfortably under good welfare conditions. The factors which influence the choice of housing system are many and include climatic considerations, the health, welfare and comfort of the animals, the provision and distribution of feed, space allocation and manure removal. This paper considers only the climatic control within the building, and discusses what constitutes an ideal environment and what needs to be considered in the provision of an optimum environment for all classes of pigs.

It is now well-established that the climatic environment has a major influence on the growth and development of an animal. It influences the rate and efficiency with which dietary nutrients are utilised for the many metabolic processes within the body. The objective should be to keep animals within their zone of thermal neutrality, since within this range of temperatures, heat production is minimal and the energy available for production is maximal. The lower and upper limits of this zone are called the Lower (LCT) and Upper (UTC) critical temperatures, respectively. Outside this zone, heat production increases and the rate and efficiency of nutrient utilisation is reduced.

Under free-living conditions, animals may compensate for variations in their climatic environment by altering their rate and pattern of feed intake, by changes in behaviour and physical activity and by seeking protection. This means changing their rate of metabolism. However, the animals' ability to alter their environment has been limited through intensification of production where they are kept in housing situations at greater stocking densities than in the past. This restricts their freedom to choose their own living conditions. Since both the nutrient intake and climatic environment are thus carefully controlled, there must be a high degree of understanding of the effects of the environment on productivity. In addition, it is important to know the consequences for long-term growth, development and reproduction if optimal climatic conditions are not provided and an understanding of the climatic needs of the pig at the different stages of production is essential.

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Defining the optimum environment

In pig production, interest lies in the determination of the range of environmental conditions within which heat loss or production is minimal, that is the thermal neutral zone. Under these conditions optimal utilisation of feed for carcass growth and development is attained. Both the lower and upper critical temperatures are often referred to as precisely defined temperatures, but no such well-defined temperatures can be obtained in practice, so that it becomes necessary to make an estimate of the 'effective critical temperatures'.

The position of the thermally-neutral zone and hence 'effective critical temperatures' on the ambient temperature scale is influenced by several animal, nutritional and environmental factors and it is important to know the extent to which temperatures below and above the critical levels increase heat loss or heat production because this indicates what reduction in performance and feed efficiency may be expected.

Animal factors

It is now well established that as body weight and insulation increase, the critical temperature decreases. Thus the new-born pig which is metabolically immature, with sparse pelage and limited body fat, has a lower critical temperature around 34°C (Mount, 1968). However, as the animal increases in size, the lower critical temperature decreases from approximately 21°C at 20kg body weight to 20 and 18°C at 60 and 100kg body weight, respectively (Holmes and Close, 1977). The critical temperature of the weaned animal, although related to body weight, is also dependent upon the age of weaning, the extent of body fat loss in the immediate post-weaning period and the level of feeding it is able to sustain after weaning. Thus for piglets weaned at two weeks of age, Close and Stanier (1984) have suggested a critical temperature of 28°C at weaning, decreasing by approximately 2°C each subsequent week. Other factors such as breed, condition of the animal and group size can also influence critical temperature and these have been reviewed by Close (1981) and Curtis (1983).

Nutritional factors

Within and above the zone of thermal neutrality, plane of nutrition influences the rate of heat production and hence critical temperature. Thus the higher the level of feeding, the higher the rate of heat production and the lower the critical temperature. For practical purposes it is therefore necessary to have an indication of the relationship between ME intake and critical temperature for different classes of animals and Table 1 has been compiled for this purpose. The results show that both the LCT and UCT values are influenced by both body weight and feeding level. These values are appropriate for individual animals and will be reduced by some 2 - 3 ^{0} C for animals living in groups.

Table 1.

Calculated limits of the lower and upper critical temperature (^0C) for pigs at different levels of feeding *(Holmes and Close, 1977)*

Body weight (kg)	Feeding level		
	M*	2M	3M
2	31 - 33	29 - 32	27 - 31
20	26 - 33	21 - 31	17 - 30
60	24 - 32	20 - 30	16 - 28
100	23 - 31	19 - 29	14 - 26
Pregnant sow			
Thin	20 - 30	15 - 27	11 - 25
Fat	18 - 30	13 - 26	8 - 24

M = maintenance energy requirement, 0.4 - 0.5 MJ ME/kg $^{0.75}$ d

Table 2.

Increase in energy and feed requirements in different classes of pigs at temperatures below LCT *(Verstegen and Close, 1994)*

Body weight (kg)	Condition	Extra energy requirement (kJ/d)	Extra feed requirement (g/d)
2	individual	47	3.6
20	individual	163	12.5
	group	160	12.3
60	individual	316	24.3
	group	310	23.8
100	individual	430	33.1
	group	417	32.1
140	thin	710	54.6
	fat	408	31.4

* If feed contains 13 MJ ME/kg

If the temperature falls below the LCT values presented in Table 2, then heat loss increases, and if energy intake is fixed, both the rate of energy retention and growth are reduced. However, several studies reviewed by ARC (1981) and NRC (1987), provided data from which the increase in heat loss and hence extra energy requirements may be calculated. If the energy content of the diet is known, then the extra feed needed to compensate for the colder environment and to ensure similar rates of retention and growth may be calculated (Table 2).

Compared with LCT, there is less information on those factors which influence the values of UCT. Christianson, Hahn and Meader (1982) estimated the UCT values of pigs as:

$$\text{UCT } (^0\text{ C}) = 34.7 - 0.33 \text{ Body weight (kg)}^{0.72}$$

However, the feed intake of the animals also needs to be considered, as indicated in Table 1.

Environmental effects

Thermal components of the environment other than air temperature influence heat loss and heat production and must be considered in practical pig production if deviations in the housing environment are to be assessed in terms of a change in the environmental or effective critical temperatures.

Air movement

An increase in air movement disrupts the thermal insulation provided by the boundary layer of air around the animal, causing an increase in convective heat loss. However, the extent to which air movement causes an increase in heat loss is dependent upon such factors as body weight, group size, and the temperature and duration of exposure (Sällvik and Walberg, 1984). Younger animals are more susceptible to changes in air movement than older animals and low draughts of air are proportionately more effective in increasing heat loss than similar changes at high wind speed (Mount and Ingram, 1965; Holmes and Mount, 1967). Mount and Ingram (1965) calculated that each 0.05 m/sec increase in air movement was equivalent in its thermal effects to a 1°C decrease in air temperature for an individual 20kg pig; for a 60kg pig, the equivalent effect was 0.10 m/sec whereas for groups of pigs it was 0.30 m/sec (Verstegen and van der Hel, 1974). Close *et al* (1981) also calculated that a 0.05 m/sec increase in wind speed was equivalent to a 1°C increase in critical temperature of single pigs. The effect of increasing air movement to 0.60 m/sec was to increase the critical temperature of the animals to 30°C, thereby indicating the beneficial effects of higher wind speeds under hot conditions. These values relate to draughts of air provided at the same temperature as that in the pen. In practice they may often be lower so that heat loss is increased, resulting in the further lowering of the equivalent air temperature.

Radiant environment

The difference between air and structure temperature determines the rate at which heat is lost by radiation and convection. Mount (1968) varied air and wall temperature independently of each other and found that when wall temperatures was below that of air, total heat loss increased as a result of increased radiation. A 1-2°C change in the temperature of the surroundings was equivalent to a 1°C change in air temperature, in agreement with that of Holmes and McLean (1977).

Relative humidity

The humidity of the air can have an important influence on the well-being of the animal at high environmental temperatures, particularly as the animal relies to a large extent on heat loss through evaporation of water. Morrison et al. (1967) have shown that as relative humidity increased from 30 to 90%, at an environmental temperature of 30°C, the animal became more dependent on cutaneous water loss, although respiration rate had almost doubled. Evaporation from the skin, as a percentage of the total, increased from 35 to 67%. The importance of cutaneous water loss, in particular that associated with wallowing, has been discussed by Ingram (1965a, b). Heitman and Hughes (1949) found that at 35°C the animal's respiration rate and body temperature were reduced and rate of gain increased on a wetted floor compared with that on a dry floor. Similar effects were experienced by increasing the rate of air velocity at these abnormally high temperatures. In terms of thermal equivalent, Holmes and Close (1977) have calculated that at 30°C an 18% increase in relative humidity was equivalent to a 1°C increase in air temperature.

Bedding and floor type

The nature of the floor determines the extent of conductive heat loss, and as approximately 20% of the animals' body can be in contact with the floor, there may be considerable heat loss through it. On a cold, uninsulated floor, the conductive heat loss may represent 20 to 25% of the animals' heat loss. Under hot conditions, however, this may be a valuable avenue of heat dissipation.

Comparisons between different floor types show the significant changes in both heat loss and critical temperature associated with bedding (Mount, 1967; Stephens, 1971; Verstegen and van der Hel, 1974). The latter calculated the effective critical temperature of groups of 40kg pigs to be 11-13°C on straw, 14-15°C on asphalt and 19-20°C on concrete slats. The degree of wetness of the floor will also have a considerable effect upon the animals' heat loss. If pigs have to lie on a wet floor, conduction to the floor and evaporation from the animals' surface will increase. This will have a beneficial effect in hot, humid conditions whereas under cold conditions the effect will be detrimental to the animal. Thus Mount (1975) has calculated that a cold, wet floor may have a thermal effect equivalent to a 7-10°C decrease in air temperature.

From the results of these various investigations it is possible to arrive at estimates of equivalent temperatures, that is the air temperatures at which similar levels of heat loss can be maintained under different housing and environmental temperatures. These equivalent temperatures are presented in Table 3 and from these the cumulative effects of the varying animal, nutritional and environmental factors on the critical temperatures have been calculated. These are presented diagrammatically for the growing pig in Figure 1 and Table 4 and show how various management and housing situations may be manipulated to supply the correct environmental conditions under both cold and hot conditions (Table 4). If the air temperature for any particular situation is less than that indicated, then energy from the feed will be used to compensate for the temperature deficiency. This leads to a reduction in growth and a deterioration in feed conversion efficiency.

Table 3. ***The extent to which deviations in the thermal environment influence the lower critical temperature of pigs*** *(Close, 1987)*

Environmental components	**Equivalent temp. (^{0}C) (to be added to air temperature)**
Air velocity (m/sec)*	
0.03 to 0.05 (individual animals)	+ 1
0.21 (groups)	+ 1
Radiant temperature	
1 to 2^{0}C	- 1
Floor material **	
straw (22 mm thick)	- 4
asphalt	- 2
concrete slats	+ 3

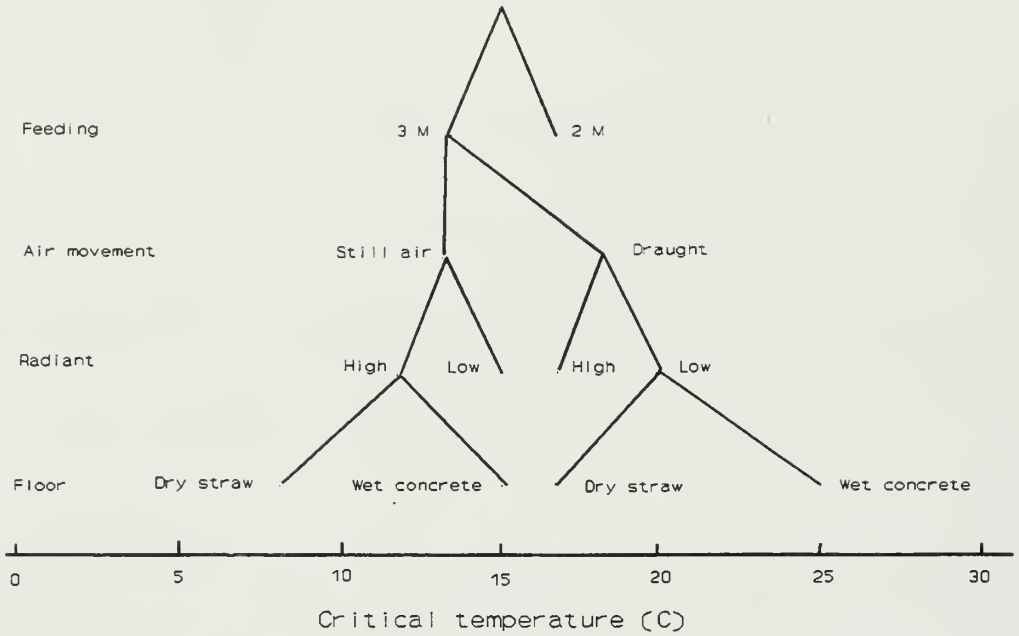
* Applicable above 0.15 m/sec.
** Comparisons made with wooden floor (Verstegen *et al.* 1973)

Table 4.
The lower critical temperature of groups of pigs in relation to differing housing conditions

	Body weight (kg)		
	20	**60**	**100**
Summer:			
Insulated house; no draughts	14	12	7
Uninsulated house; no draughts	17	15	11
Winter:			
Insulated house; draughts	18	16	13
Uninsulated house; draughts	23	20	17
Summer:			
Insulated house; straw bedding	10	8	2
Winter:			
Uninsulated house; cold/wet concrete	29	25	22

(Values appropriate to a feeding level of 3M (M = 440 kJ ME/kg $^{0.75}$ d) (Mount, 1975)

Figure 1.



Environmental effects on LCT *(Close, 1981)*

Fluctuating temperatures

The extent to which animals can tolerate fluctuating temperatures are primarily dependent upon body weight and food intake. Le Dividich (1981) varied the air temperature by ± 3^{0}C each hour throughout the 24-h period and clearly demonstrated that the post-weaning performance of young pigs was less than that when the temperature was maintained constant. The incidence of post-weaning scours was also increased. On the other hand, Morrison, Heitman and Givens (1975) found that neither growth rate nor food conversion efficiency of 60-kg pigs was affected by a 10 or 20^{0}C diurnal temperature, when compared with a constant temperature equal to the mean of the cycle if the mean temperature was within the thermal neutral zone. However, when a constant or diurnal temperature pattern was maintained at 6^{0}C above the optimum, then performance declined with the 20 ^{0}C cycle range. It is likely that the performance was reduced due to heat stress during the periods of extreme temperature which rose to 40^{0}C at its highest value. Since the pigs were fed *ad libitum*, one possibility is that the effect was mediated through a change in food intake, rather than a direct effect of temperature *per se*. Thus, the animals on restricted food intakes may be less likely to tolerate larger fluctuation in temperature than those fed *ad libitum*. Lopez *et al* (1991), showed that finishing pigs consumed less feed and grew more slowly in a hot, diurnal temperature than in a constant thermo-neutral environment. In a cold, diurnal temperature, they consumed more feed, but grew more slowly. These results suggest that for growing pigs, temperature fluctuations of more than 3-5^{0}C around the mean should be avoided. Evidence also suggests that since pigs have a diurnal pattern of heat production, with the lowest heat production occurring at night, they can tolerate colder temperatures at night, especially when housed in groups and given the opportunity to huddle (McCracken and Caldwell, 1989; Brumm, Shelton and Johnson, 1985; Brumm and Shelton, 1991).

Environmental effects upon production characteristics

Energy metabolism (including protein and fat deposition)

The environmental conditions within which animals are housed influences the extent to which ME intake is utilised for maintenance, on the one hand, and energy retention or growth on the other. At any given energy intake, exposure to temperatures outside the zone of thermal neutrality increases the maintenance energy requirements (ME_m), with a concomitant reduction in the energy available for production. From the results of various investigations, ARC (1981) calculated that the mean increase in ME_m at temperatures outside the zone of thermal neutrality was 20 kJ/kg $^{0.75}$ per day. However environmental temperature is not the sole climatic variable influencing ME_m. Close *et al* (1981) have shown that an increase in air movement from 0.03 to 0.56 cm/sec increased ME_m from 706 to 881 kJ/kg $^{0.75}$ per day at 10°C, from 490 to 715 at 20°C and 517 to 625 at 30°C. This considerable increase in ME_m indicates the extent to which energy in the feed is used for thermoregulatory purposes.

If ME_m increases then at any given energy intake there must be a change in the energy available for production and hence energy deposition as protein and fat. The results of a number of experiments suggests that protein deposition is remarkably independent of environmental temperature (Fuller and Boyne, 1971; Close *et al*, 1978; Phillips *et al.* 1982) indicating that at similar levels of intake the increase in ME_m is achieved at the expense of fat deposition (Table 5). However, fat deposition is very dependent upon the environmental conditions within which the animals are maintained, so that at any given intake, the highest depositions occurred between 23 and 25°C. Above 25°, fat retention was reduced in association with the hyperthermal rise in heat production. The temperature-dependent change in fat deposition was greater than that of protein and was equivalent to a 28 g/day reduction in feed intake, compared with an equivalent reduction of only 4 g/day for protein.

Table 5.

The effects of temperature on protein and fat gain in growing pigs (g/1°C decrease in temperate)

Protein	Fat	Source
2.4	4.9	Fuller & Boyne (1981)
-	2.4	Verstegen *et al* (1973)
0.2 - 1.2	3.6 - 6.4	Close *et al* (1978)
1.4	-	Philips *et al* (1982)

Growth rate

The depression in growth rate associated with a decrease in environmental temperature results from an increase in the animals' maintenance energy requirement and a reduction in the rate at which protein and fat are deposited (Table 5). When the environmental temperature falls below the lower critical temperature the heat production rises by between 2 and 4% per 1°C

fall. These figures give an estimate of the demands made by the environment on the pig to produce heat, and this heat must be derived from dietary nutrient intake. The question which arises is, how significant is this rise in environmental demand for the growing pig's feed conversion and growth rate and there are many estimates indicating the extent to which growth rate is diminished when the environmental temperature is reduced(Close,1981; Curtis, 1983). From a review of the literature Verstegen *et al.* (1977) calculated over a wide range of breeds, feeding levels and housing conditions that growth rate was decreased by 8.1 g/day for each 1°C decrease in temperature below the critical level. To compensate for this they calculated that feed intake under *ad libitum* feeding conditions increased by 19.5 g/day for each 1°C below 15°C.

In many situations it is not always possible to feed pigs *ad libitum* and for practice it is important to know how much extra feed is needed to maintain similar levels of production both below and within the zone of thermal neutrality. Table 6 has been compiled for this purpose and indicates that the additional feed requirements during the growing/fattening phase increase between 22 g/day per 1°C at 20kg to 43 g/day per 1°C at 100kg body weight. These requirements are useful in determining whether it is more economical to keep the environmental temperature for growing/finishing pigs at or above their critical temperature and hence spare feed, or to increase the animal's feed allocation in response to the cold stress and hence save the costs of providing additional heating in the building. The decision will depend upon the costs of feed energy relative to that of fuel energy. For sows Geuyen *et al.* (1984) have calculated an additional feed requirement of 75 and 40 g/day per 1°C drop in temperature when kept either individually or in groups, respectively. This decrease in requirements reflects the beneficial effects associated with grouping.

Table 6.

The reduction in growth and the increase in feed requirements necessary to maintain growth rate per 1°C below LCT

	Body weight (kg)		
	20	**60**	**100**
Reduction in growth rate (g/d)	14	12	8
Increase in feed requirements (g/d)	22	32	43

(Verstegen and Close, 1994)

Carcass effect

The variations in the protein and fat gains of the animal reflect changes in carcass composition. In agreement with the changes in protein and fat deposition, it may be concluded from both chemical analysis and carcass appraisal studies, that cold environments results in leaner carcasses (Holmes and Close, 1977; Close, 1981). Exposure to hot environments also influences carcass composition, but only through its effects on the animal's feed intake. Temperature *per se* influences the morphological characteristics of the animal. Pigs kept under cold conditions have shorter ears, denser coats, shorter limbs and fewer blood vessels in their

skin (Fuller, 1965; Dauncey *et al.* 1983). Carcass length may also be reduced (Holme and Coey, 1967). In the fat depots of the animal, prolonged exposure to colder environments produces a high degree of unsaturated fatty acids which can influence the melting point and physical characteristics of the fat (McGrath *et al.* 1968; Fuller *et al.* 1974). Hot conditions, on the other hand, increase the water binding capacity of the muscle (Hacker et al, 1973) and this may influence muscle quality. Within breeds of animals, high environmental temperatures cause the phenomena known as malignant hyperthermia syndrome, which produces a pale, soft and exudative condition known as PSE in the muscle after slaughter.

Feed intake

Given access to an *ad libitum* supply of feed, the animals' voluntary food intake decreases with increase in air temperature. From a review of several experiments, Close (1989), suggested that the relationship between energy intake and environmental temperature was best described by the equation:

$$y = 9.6 + 0.075\ x_1 + 0.52\ x_2 - 0.012\ x_1\ x_2$$

Where y is the ME intake in MJ/day, x_1 is the temperature (^{0} C) and x_2 is the body weight (kg). ME intake therefore decreases by 0.12 and 1.12 MJ/day for each 1 ^{0} C reduction in temperature for pigs of 20 and 100 kg body weight, respectively.

More recently, Rinaldo and Le Dividich (1991), calculated that the relationship between feed intake and temperature to be:

$$y = 16.8 \times \text{Temperature} - 0.8 \times \text{Temperature}^2 + 1163.$$

y is the feed intake in g/day of a diet containing 12.4 MJ ME/kg and temperature is in ^{0}C.

Temperature has a greater effect on the voluntary feed intake of the sow than on the growing or finishing pig. For example, Stansbury, Mc Glone and Tribble (1987) reported that at 30 ^{0} C, lactating sows consumed only 4.2 kg/day, compared with 6.46 at 18 ^{0} C. As a consequence, the animals lost considerable weight during lactation. However, they similarly showed the importance of evaporative or convective cooling in increasing the appetite of sows under hot conditions.

Temperature is not the sole component of the environment which influences appetite. Other components which are equally important are air movement and relative humidity. However, one component which is often over-looked and can significantly influence feed intake is stocking density or space allocation. This topic has been reviewed by Kornegay and Notter (1984) and NRC (1987). From these studies it may be calculated that each 0.1 m ^{2} reduction in space allocation results in a 0.65 MJ/day reduction in energy intake. The space allowance for optimum feed utilisation was 0.40 m^2 for weaned piglets, 0.60 m^2 for growing pigs and 1.00 m^2 for fattening pigs. The extent to which the different components of the environment influence appetite in groups of 60 kg pigs is presented in Table 7.

Table 7.

Environmental effects on voluntary feed intake in growing pigs (60kg)

Environmental component	Change in ME intake (MJ/day)
Air temperature (1^0C)	0.65
Air movement (10 cm/sec)	0.52
Relative humidity (0.1)	0.47
Ammonia concentration (10 ppm)	0.36
Space allocation (0.1 m^2 per pig)	0.65

(Close, 1989)

Climatic effects upon reproduction

The environment influences sow productivity by influencing fertility, through its effects upon ovulation rate and embryonic mortality, and by altering the transfer of dietary nutrients within the maternal body and gravid uterus. The two main environmental components affecting fertility are ambient temperature and day length. Thus ovulation rate is significantly reduced at high environmental temperatures although it is possible that the observed reduction may be due to the reduced feed intake under these conditions rather than the direct effect of temperature *per se* (Wettemann and Bazer, 1985). However after the first three weeks of pregnancy, that is after the implantation period, the embryos appear to become resistant to heat (Steinbach, 1976). During the last three weeks of pregnancy, the sow becomes susceptible to heat and prolonged exposure at farrowing can lead to exhaustion and sometimes death (Omtvedt *et al*, 1981).

During pregnancy there is optimum utilisation of dietary energy for both net maternal and gravid uterus gain when the sow is maintained within thermal neutral conditions. It is generally assumed that the lower critical temperature of a normal sow at normal levels of feeding is within the range 18-20°C (ARC, 1981). However if the environmental conditions are too cold and if feed intake is limited, then the dietary nutrients are unable to meet all metabolic demands. Mobilisation of body tissue may then occur and this limits both maternal body and gravid uterus gain. Repeated and prolonged exposure to these conditions will result in low litter sizes, piglets of low birth weights and a severely emaciated, infertile sow. Such a condition, the 'thin sow syndrome' has been reported in practice.

Although heat stress during the first three weeks of pregnancy can have a serious effect upon reproductive efficiency, during the final weeks it can cause thermal discomfort through an increase in rectal temperature and the respiration rate of the sow. Exposure to heat at this stage may also increase the number of still-born piglets (Omtvedt *et al.* 1976; Steinbach, 1971). This susceptibility to heat stress in late gestation may be associated with the increased

metabolic rate of the sow which is alleged to occur at this time. At farrowing pigs are also susceptible to exhaustion and subsequent death after exposure to elevated temperatures (Omtvedt *et al.* 1971).

In terms of the thermal environment, the requirements of the lactating sow and those of her piglets are at variance with one another. Since the piglet nutrients needs can only be met through the milk supply of the mother, it follows that factors controlling maternal feed intake during lactation will determine the rate and efficiency of piglet growth. Thus exposure to high environmental temperatures reduces feed intake, limits milk supply and increases the loss of body fat from the sow so that the weight of the piglets at weaning may be reduced, as has been reported under tropical conditions by Steinbach (1976). On the other hand, the piglets require a warm environment for optimum growth and development. This conflict of requirements is apparent from the experiments of Lynch (1977) who showed that sows maintained at an environmental temperature of 27°C decreased their feed intake by 12% relative to that at 21°C. Even though the piglets at the higher temperature consumed larger quantities of creep feed to compensate for the reduced milk yield, the overall effect was a lower piglet body weight when weaned at 4 weeks of age, 6.76 kg at 27°C compared with 7.75kg at 21°C.

There is little evidence to suggest that cold conditions impair the reproductive function of the boar, provided sufficient feed is given to meet the nutrient requirements essential for normal growth and body development. However under hot conditions, the environment influences boar performance through its effect upon the retardation of sexual development, reduced libido, reduced sperm motility and a higher proportion of abnormal sperm cells (Christenson *et al.* 1972). These traits did not appear to become evident until some 16-30 days after exposure to heat and may persist for as long as 60-64 days post-treatment.

Practical implications for pig housing and conclusions

It is obvious that pigs will continue to be housed in buildings of different designs. Therefore, the general requirement for farming practice is to determine the range of environments and nutrition which allow maximum efficiency of feed utilisation. This necessitates the determination of the zone of thermal neutrality for all classes of livestock, and those factors which influence it. If the environmental conditions fall below or above this zone then growth rate is reduced, with concomitant effects upon feed conversion efficiency. Under cold conditions, where the animal may be below its LCT, actions such as structural improvements to the buildings, the provision of supplementary heating or increasing the animal's feed allocation may be taken to improve the environment. The decision will depend upon the cost of fuel energy relative to that of feed energy, and hence the prevailing economic circumstances.

In hot conditions, where the air temperature exceeds the higher critical temperature, the solution is not so simple since the requirement of the animal is to limit its heat production in order to avoid hyperthermia. It achieves this by reducing its feed intake and pattern of eating, by changes in posture and behaviour and by seeking shelter. By reducing feed intake and by

eating 'on a little and often basis' the heat increment associated with feeding is reduced. Feeding behaviour and drinking also change so that the animal drinks more water. As the animal relies on its evaporative heat exchange for the maintenance of homeothermy it follows that ways to enhance water vapour renewal help adaptation and increase production. The use of wallows, hoses or automatic sprinklers and the control of relative humidity have been shown to improve productivity under tropical conditions. The provision of draughts of air around the animal may also be effective in alleviating heat stress.

Housing can therefore reduce the "thermal stress" of animals in both cold and hot conditions and improve their performance. It also allows better control of both the quantity and quality of feed, a reduction in the energy expenditure and improvement in animal comfort and welfare. However the costs of construction, maintenance and labour must be set against any improvement in performance. It is likely that the high cost and quality of the end-product, the improved use of feed and resources, the improvement in fertility and fecundity and the increase in survivability will far outweigh these structural costs. In this respect, studies on the climatic needs of the pig have played an integral role in permitting a rational approach to be used in the design of these buildings and in deciding the type of housing and management and husbandry practices most suited to the different climatic regions and types of production.

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FEEDING FINISHING PIGS FOR OPTIMAL LEAN GROWTH AND MAXIMAL ECONOMIC RETURNS

DAVID H. BAKER

Introduction

Nitrogen and phosphorus pollution of the environment have become important, and animal production must do its part to minimize excessive nitrogen and phosphorus output in animal excreta. Geneticists have done their part in providing a new generation of pigs that are capable of producing protein gain at greater efficiencies than ever before. The nutritionist now must design feeding programs that can take advantage of the "new" genetics to produce a palatable product with a high lean:fat ratio, and in the process produce this product in a way that maximizes use of amino acids for protein accretion, minimizes excretion of nitrogenous waste products, and maximizes economic returns.

Protein is a costly item in pig diets, and this makes maximizing the efficiency of protein and amino acid utilization very important. How can one maximize lean meat production with the absolute minimum intake of amino acids? Clearly, diets containing amino acids at minimally required levels (for maximal lean growth) with minimal excesses, is a critically important factor. Use of ideal protein concept in feed formulation is very helpful in achieving this end. It is important to remember that of the amino acids used in protein synthesis, at least 60% are derived from body protein degradation. Thus, the nutritionist must design dietary amino acid profiles that will complement the profile being provided by protein turnover.

Ideal Protein for Pigs

Theoretically, an ideal pattern of amino acids should exist for each physiological function, but clearly, the ideal pattern will be different for each function, i.e., maintenance, protein accretion, reproduction and lactation. For meat production, amino acid requirements can be separated into that required for protein accretion and that required for maintenance. Moughan (1989) and Fuller (1991) described maintenance as comprising 1) urinary excretion of unmodified amino acids, 2) use of amino acids as precursors for other essential body metabolites (eg., creatine from arginine and glycine; taurine and glutathione from cysteine, or indirectly from methionine; thyroxin, melanin and catecholamines from tyrosine, or indirectly from phenylalanine; serotonin from tryptophan; nucleic acids and choline from glycine or serine; carnitine from trimethyl lysine;

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nitrous oxide and polyamines from arginine; carnosine from histidine), 3) amino acids lost from integuments and epidermal structures, 4) obligatory oxidation of amino acids, and 5) amino acids lost from gastrointestinal epithelia (mucous, mucosal cells, digestive enzymes).

Mitchell (1964) discussed the concept of an ideal protein or perfect amino acid balance in 1964. Thus, he recognized that chemical scoring (Mitchell and Block, 1946) using egg protein as the ideal standard, was flawed. Indeed, egg protein is too rich in essential amino acids, with isoleucine, for example, being present at twice the level that most animals require. Cole (1978) proposed that diet formulation for pigs could be done on the basis of ideal amino acid ratios, and ARC (1981) subsequently described ideal ratios of amino acids for pigs. The ideal pattern received considerable attention over the next 12 years (Wang and Fuller, 1989; 1990; Fuller et al., 1989; Chung and Baker, 1992a), and in 1992 Baker and Chung (1992) proposed ideal amino ratios for pigs in three different weight classes (Table 1). Based upon additional calculations as well as recent empirical research (Baker, 1993; 1994; Hahn and Baker, 1995) our original ratios for later growth phases have been modified somewhat. Because the maintenance requirement for lysine is low relative to maintenance requirements for certain other amino acids (eg., threonine, cystine), ideal ratios of certain amino acids for young pigs cannot be applied without adjustment to older market-type pigs.

Of the total requirement for a given amino acid, protein accretion comprises well over 90% of the need for pigs weighing 10 kg, but as pigs approach slaughter weight maintenance assumes greater prominence in the total requirement for an amino acid (Fuller et al., 1989; Black and Davies, 1991; Chung and Baker, 1992b; Baker, 1994). Thus, while the ideal ratio of sulfur amino acids (SAA, i.e., methionine + cystine) to lysine is 60% for 10-kg pigs (Chung and Baker, 1992a) the ideal ratio for the maintenance component of that requirement is much higher (Fuller et al., 1989; Fuller, 1994). Indeed, in every species where requirements for maintenance have been specifically studied, including studies with humans, the SAA requirement has exceeded the lysine requirement (Baker and Han, 1993). With an increasing contribution from maintenance as an animal grows toward slaughter weight, the ratio of SAA:lysine must increase, probably in a straight-line fashion, as a growing pig advances from 10 kg to 110 kg. Gut losses of SAA particularly cystine, account for less than half of the maintenance need for SAA, but gut losses of threonine account for 75% of the maintenance need for threonine (Fuller, 1994). Estimates of the threonine requirement for swine maintenance suggest that it is considerably higher than the maintenance need for lysine (Baker et al., 1966; Fuller, 1994) with the threonine:lysine ratio being about 150%. Also, the ideal tryptophan:lysine ratio for maintenance per se is greater than the ideal ratio for protein accretion per se (Fuller et al., 1989; Fuller, 1994).

Least-cost diet formulation on an ideal protein basis can be influenced significantly by the ratios used. Work by Burgoon et al. (1992) and our work with 15-kg pigs (Han et al., 1993) could be interpreted as suggesting that 17% of the true digestible lysine as tryptophan is just as effective for young pigs as higher ratios. Whether one uses 17 → 18 → 19% (starting → growing → finishing), or instead, higher ratios (Fuller, 1991) for a tryptophan:lysine ratio, can have profound effects on diet formulation and, in particular, on quantities as well as sources of both lysine and tryptophan that go into finished pig feeds. Interestingly, the situation could be quite different for barley/wheat-soybean meal diets such as those used outside the U.S. Threonine and lysine are

the important amino acids in these diets, and threonine unlike tryptophan is not abundant in soybean meal (nor in barley or wheat, either). Thus, the threonine:lysine ratio in soybean meal is 64% which is lower than that prescribed in ideal protein.

Use of Ideal Protein to Formulate Pig Diets

Whether using total or true digestible lysine requirement data, one can accurately formulate pig diets. Clearly, controversy surrounds the topic of digestibility, i.e., whether to use apparent, true or "real" digestibility values, or whether "bioavailability" (growth assay) values should be used for some ingredients like cottonseed meal. With corn-soybean meal diets, the question is not real important because true digestibility values for the key amino acids (lysine, threonine, tryptophan and SAA) are about the same. Thus, using either true digestible lysine or total lysine as a base, results in similar ratios and therefore in similar predicted requirements.

If diet formulation is done using apparent digestibility data (i.e., for requirements as well as for feed ingredients), problems are encountered. The apparent digestibilities of threonine and tryptophan are lower than the apparent digestibility of lysine, and this is true for virtually all types of diets. Also, apparent amino acid digestibility values for cereal grains are underestimated, because at lower protein levels endogenous losses contribute heavily to total ileal losses of amino acids (Fan et al., 1995; Fan and Sauer, 1995). Thus, one can calculate that the ideal ratios for threonine on an apparently digestible basis are 58 → 60 → 62% (of apparently digestible lysine) for starting, growing and finishing pigs, respectively, instead of the 65 → 67 → 70% values (Table 1) that apply when formulating diets on a total or true amino acid digestibility basis. The other amino acid whose ideal ratio changes importantly when formulating on an apparent digestibility basis is tryptophan. Apparently digestible tryptophan as a percent of apparently digestible lysine calculates to be 15 → 16 → 17% instead of 17 → 18 → 19% (true or total amino acid basis) for starting, growing and finishing pigs, respectively.

Another factor that can cause overestimation of dietary needs for amino acids other than lysine is use of unrealistic requirement values for lysine. There has been a tendency for some to assume lysine requirement values for finishing pigs that are higher than they really are. Thus, with either cheap lysine or cheap soybean meal it is not uncommon for dietary levels of lysine to increase. If excess (or "safety factor") lysine levels are fed, one should ratio threonine, SAA and tryptophan to the "real" lysine requirement, not to the excess dietary lysine level, in calculating dietary ratios of threonine, SAA and tryptophan. If such ratios fall below 70, 65 and 19%, respectively, for finishing pigs (Table 1), then supplementation with one or more of these amino acids (or with more soybean meal) is necessary.

Realistic Lysine Requirements for Finishing Pigs

We have recently been working on apparently digestible and total lysine requirements of finishing barrows and gilts during two growth periods, 50 to 90 kg and 90 to 110 kg (Hahn et al., 1995). The pigs we have used are of PIC line 26 x Camborough 15 breeding. At a kill weight of 250 lb. these pigs typically have 10th-rib loin-eye areas of 6.0 sq in. (barrows) and 6.5 sq in. (gilts) with 10th-rib fat depths of 1 to 1.1 in. (barrows) and .9 to 1.0 in. (gilts). Using a determined

lysine digestibility of 85% in a corn-soybean meal diet, we have translated our determined apparent digestible lysine requirements to total lysine requirements (Table 2). Requirements for threonine, methionine + cystine and tryptophan were estimated by multiplying ideal ratios (70, 65, 19%) x the total lysine requirement. The requirements for these amino acids are generally met when a 15.2% CP corn-soybean meal diet is fed during early finishing and when a 13.2% CP diet is fed during late finishing (Table 3). Moreover, within a given genetic line, stress-related decreases in voluntary feed intake (e.g., crowding, disease, heat stress) lower lean growth potential and thus are not likely to cause increased requirements expressed in terms of diet concentration (% of diet or % of calories).

Genotypes that have higher lean:fat ratios than the PIC pigs used in our research (Hahn et al., 1995; Hahn and Baker, 1995) will have higher amino acid requirements and will therefore require higher protein levels in corn-soybean meal diets than those shown in Tables 2 and 3. On the other hand, pigs with less potential for lean growth will have lower requirements than those presented in Tables 2 and 3.

Several prominent feed companies have been conducting trials with pigs that are as lean or leaner than those used in our research at the University of Illinois. Also, Meyer and Bucklin (1994) have conducted protein/lysine level trials at the University of Florida involving pigs that had lower lean growth potential than the PIC pigs used in our Illinois trials. The Florida pigs at 250 lb. had average loin-eye areas of 5.3 sq in. and average 10th-rib fat depths of 1.2 in. when fed during the Fall-Winter period, but they were fatter (4.9 sq in. LEA and 1.3 in backfat) when fed under heat-stress conditions in the Summer months. Regardless of feed intake level (pigs fed in the summer ate 10% less feed), dietary lysine levels in excess of 1988 NRC recommendations for finishing pigs (i.e., .60% of diet) did not elicit a response in performance or carcass merit. Feed company trials with lean pigs have generally resulted in recommended lysine levels for finishing pigs ranging from our recommendations (Table 2) to slightly higher levels (.80%, 120-200 lb.; .65%, 200 to 280 lb.).

In designing diets that will meet ideal levels of lysine, threonine, SAA and tryptophan with minimal excesses of any of these amino acids, crystalline lysine is necessary. Moreover, if economical to do so, use of crystalline threonine, methionine and tryptophan (all available in feed-grade form) would minimize dietary excess amino acids even more, and as a result would reduce nitrogen output in both feces and urine. Careful calculations reveal, however, that if using lysine supplementation alone, the upper limit of use is about .10% (equivalent to 2.5 pounds of feed-grade lysine per ton of complete feed) for corn-soybean meal diets. Thus, if one uses more than .10% of added lysine, ideal ratio calculations reveal that threonine becomes limiting first, followed closely by SAA and tryptophan.

Feed Intake Influences on Amino Acid Requirements

Feed intake increases or decreases that are caused by caloric density changes or by the inherent capacity of a given genetic line for lean growth potential will change amino acid requirements. But how does one translate a daily requirement (eg., for lysine) determined at one feed intake to another feed intake. The evidence is mounting that stress-related decreases in feed intake, within

a genetic line, will lower the lean growth potential of the pigs in question. Stresses such as crowding (Hahn et al., 1995; Kornegay et al., 1993), increased numbers of pigs per pen (Chapple, 1993; Hahn et al., 1995) heat stress (Han and Baker, 1993; Meyer and Bucklin, 1994) and disease (Stahly, 1994) have been shown to depress feed intake and to also lower lean growth potential.

To meet the daily lysine need for virtually all of the gilts in our University of Illinois PIC pigs required 21.1 g/d lysine during early finishing (120 to 200 lb.) and 17.2 g/d during late finishing (200 to 260 lb.) [Hahn and Baker, 1995; Hahn et al., 1995]. During both early and late finishing under conditions of minimal environmental stress, the gilts consumed an average of 6.2 lb. of feed per day (3% fat in diets). This calculates to be a dietary concentration of .75% for early finishing and .61% for late finishing. If these pigs are now stressed such that their daily feed intake falls to 5.5 lb./d, do they still require 21.1 g/d of lysine (.85% of diet) during early finishing and 17.2 g/d (.69%) during late finishing? Or alternately, do they now require 18.75 g/d (.75%) during early finishing and 15.25 g/d (.61%) during late finishing? The evidence would suggest that the stressed gilts in question no longer require 21.2 g/d and 17.2 g/d during early and late finishing, respectively. Thus, their lean gain potential has been reduced, so their daily lysine needs are reduced as well. In fact, the stressed gilts consuming 5.5 lb. of feed per day may still require close to .75% and .61% lysine during early and late finishing, respectively.

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Table 1. Ideal Pattern of Indispensable Amino Acids for Pigs in Three Separate Weight Categories[a]

Amino acid	Ideal Patterns (% of lysine)		
	10 to 40 lb.	40 to 120 lb.	120 to 260 lb.
Lysine	100	100	100
Threonine	65	67	70
Tryptophan	17	18	19
Methionine	30	30	30
Cystine	30	32	35
Methionine + Cystine	60	62	65
Isoleucine	60	60	60
Valine	68	68	68
Leucine	100	100	100
Phenylalanine + Tyrosine	95	95	95
Arginine	42	36	30
Histidine	32	32	32

[a]From Chung and Baker (1992), Baker and Chung (1992), Baker (1993), and Baker (1994); ratios are expressed on a true digestible basis.

Table 2. University of Illinois Recommended Dietary Requirements for Key Amino Acids for Finishing Pigs[a] Fed Corn-Soybean Meal Diets[b]

		Barrows			Gilts		
Amino Acid (%)[c]	Ideal Ratio[d]	Early Finisher 120-160 lb.	Middle Finisher 160-210 lb.	Late Finisher 210-260 lb.	Early Finisher 120-160 lb.	Middle Finisher 160-210 lb.	Late Finisher 210-260 lb.
Lysine	100	.70(.67)	.63(.60)	.56(.53)	.78(.74)	.69(.65)	.58(.55)
Tryptophan	19	.13(.13)	.12(.12)	.11(.10)	.15(.14)	.13(.12)	.11(.10)
Threonine	70	.49(.47)	.44(.42)	.39(.37)	.55(.52)	.48(.46)	.41(.39)
Met + Cys	65	.46(.44)	.41(.39)	.36(.34)	.51(.48)	.45(.42)	.38(.36)

SOURCE: Department of Animal Sciences, Swine Nutrition Group (David Baker, Robert Easter, Gilbert Hollis).

[a]High lean-gain genetics (51% lean yield).

[b]With 3% added fat or without (parentheses) any fat supplementation.

[c]Total dietary requirement.

[d]Expressed as a percentage of the total lysine requirement.

Table 3. Corn-Soybean Meal Diets for PIC Finishing Pigs (Mixed-Sex Feeding)[a]

Body weight	Option I	Option II[b]
120 to 200 lb.	15.2% CP	13.8% CP + .1% L-lysine
200 to 260 lb.	13.2% CP	11.8% CP + .1% L-lysine

[a]Assumes 3% fat in diet.

[b].1% L-lysine provided by .127% feed-grade lysine•HCl (78.8% L-lysine activity).

WHY DO WE OVERFEED PIGS?

Robert A. Easter and Hans H. Stein

Introduction

No one would challenge the statement, "Pigs must eat in order to grow." However, there can be significant discussion around the question, "How much should the pig eat?" The traditional, North American response has been to let them eat freely. And, feeders, pens and diets have been designed to encourage maximum feed consumption. Pigs usually do grow faster if they can be encouraged to eat more. But, is maximum growth rate always consistent with maximum economic return? That depends on the relationship between feed intake and the composition of growth. This paper will offer some thoughts on that relationship.

Energy Intake and Growth Composition

Feed provides essential nutrients and energy. If one assumes that diets are formulated to be adequate in the necessary nutrients regardless of intake, then the discussion can be focused exclusively on energy. Clearly, not all consumed energy is available for growth. There are losses due to inefficiencies in digestion and metabolism. Additionally, a portion of the energy must be used for maintenance. The remainder is available for growth and is used primarily of lean and fat tissues. The relative rates of lean and fat growth determine the percentage lean in the animal at slaughter and, value.

Whittemore (1987) is often credited with the hypothetical representation of growth shown in figure 1. The Whittemore model seeks to describe the effect of increasing daily energy intake on total growth rate and on the growth of lean and fat tissues. As energy intake increases above that required for maintenance, i.e., zero growth, a portion of the consumed energy is used for lean growth and a lesser amount is used for obligatory fat growth, e.g., kidney fat. This relationship continues without appreciable change until the pig's lean growth potential is realized. Energy consumption in excess of that required to achieve maximum lean growth, is used for fat synthesis.

The Whittemore (1987) model is supported by a large body of empirical evidence. Classical studies of pig growth, c.f. McMeekan (1940) and Fowler (1968), demonstrated the capacity of the pig to vary body fat content in response to dietary energy. Over the past decade, much research effort has been devoted to the development of compounds, such as the beta adrenergic agonists and porcine somatotropin, to alter the partitioning of energy in favor of lean growth.

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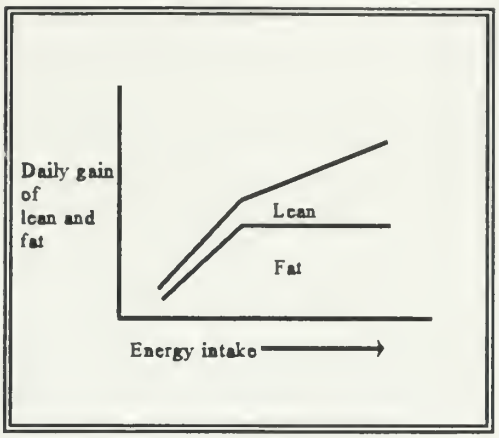
Figure 1 Partitioning of energy to lean and fat growth. After Whittemore (1987)



Recent data has continued to confirm the wisdom of restricting energy intake in the finishing phase in order to increase carcass the proportion of lean in the carcass. The data, table 1, from Campbell et al. (1985) illustrate the point.

Table 1. Effect of energy intake on the growth of Lean and fat tissues in 100 to 198 lb finishing pigs[1]

Metabolizable energy, kcal/d	Lbs/day of a corn-soy diet (approximate)	Growth rate of tissue, grams/day			
		Entire males		Gilts	
		Protein	Fat	Protein	Fat
5497	3.7	69.4	79	63.4	125
6572	4.5	94.8	150	84.5	208
7887	5.4	129.5	184	103.0	279
8962	6.2	130.0	304	102.0	332
9990	6.9	132.0	352	99.0	371

[1] Campbell et al. (1985)

The daily energy level was varied between 5,497 kcal and 9,990 kcal, which is roughly the equivalent of increasing the daily ration of a corn-soybean meal diet from 3.7 to 6.9 lbs. Diets were formulated to insure that amino acid intake did not limit growth at any level of feeding. Protein growth increased in both entire males and gilts as energy intake increased. Maximum protein growth was achieved at 7,887 kcal of daily energy intake in both genders. Fat growth continued as energy intake increased.

Although the work cited above addresses intake up to maximum voluntary consumption, it does not give consideration to intake beyond the normal upper limit. Pekas (1983), working at the USDA Center in Nebraska, developed a technique for overfeeding pigs through a tube surgically installed in the greater curvature of the stomach. He used this technique to provide a level of feeding well beyond that which would be consumed voluntarily. He reported marked increases in gain (Pekas, 1985). More importantly, carcass composition remained constant, i.e., there was an proportional increase in both protein and fat growth. This finding supported a hypothesis that extra muscle could be obtained if pigs could be caused to eat more.

We thought it useful to challenge this hypothesis and a series of experiments were conducted at the University of Illinois. Pigs were fitted with stomach cannulas and allowed to recover from the surgery. Littermates to the cannulated pigs were retained as controls to verify that surgical modification had not altered growth. A group of pigs were killed at the beginning of the experiment and the bodies were ground and analyzed chemically to establish initial composition. The remaining pigs were fed for four weeks, killed and the bodies analyzed. The comparison of initial and final composition data were was used to establish the net gain in fat and protein content. The results of an initial experiment (Newcomb et al., 1993) are described in table 2.

Table 2. Effect of hyperalimentation on Growth and composition of growth in 70 lb pigs[1]

Item	Noncannulated pigs fed ad libitum	Cannulated pigs fed ad libitum	Cannulated pigs hyperalimented to 120% of ad libitum
No. of pigs	9	9	20
Avg. daily feed, lbs	4.79	4.70	5.67
Avg. daily gain, lbs	1.91	1.95	2.22
Gain/feed	.41	.43	.40
Protein gain, lbs	5.00	5.31	5.30
Fat gain, lbs	9.00	8.88	11.71

[1] Newcomb et al. (1993)

Cannulated pigs voluntarily consumed an amount equal to noncannulated controls and their growth rates were similar. As one would expected, the cannulated pigs provided with 120% of the feed voluntarily consumed by the control animals grew faster. Note, however, that providing 20% more feed did not increase protein gain. However, the extra feed resulted in a dramatic increase in fat gain.

It is reasonable to ask if there are circumstances where pigs might benefit from increased energy intake. It has been suggested (Michael Ellis, personal communication) that some very lean

genotypes may have a level of voluntary feed intake that fails to provide the energy needed to support maximum protein growth. That hypothesis has not been tested. However, Newcomb (1990) did examine the effect of hyperalimentation in pigs with increased lean growth due to treatment with recombinant porcine growth hormone.

The protocol for this experiment was similar to that described previously with the exception that some pigs were treated with 3 mg per day of porcine somatotropin (PST). The results are shown in table 3. Observe that there was a reduction in voluntary feed intake when non-cannulated pigs were treated with PST. This is a consistent effect of somatotropin treatment and leads to the question, "Does feed intake limit protein growth in PST-treated pigs?" When PST-treated pigs were hyperalimented to the level of feed consumed by non-cannulated pigs injected with a saline placebo, there was a marked increase in daily gain. Note however, that this increase in gain was accounted for by an increase in fat deposition, not by an increase protein gain. Thus, even in pigs that have enhanced lean growth, the level of voluntary consumption of a corn-soybean meal diet provides sufficient energy to maximize lean gain.

Table 3. Effect of hyperalimentation on growth Composition in pigs treated with porcine somatotropin (pst)[1]

	Treatments			
Item	Non-cannulated ad libitum-fed saline injection	Non-cannulated ad libitum-fed PST injection	Cannulated ad libitum-fed PST injection	Cannulated hyperalimented PST injection
No. pigs	5	5	6	8
Daily feed, lbs	7.50	6.66	6.46	7.52
Daily gain, lbs	2.28	2.50	2.61	3.10
Gain/feed	.31	.38	.42	.42
Protein gain, lbs	14.03	17.46	18.70	19.09
Fat gain, lbs	35.64	26.20	22.50	31.30

[1] Newcomb (1990)

Are there any circumstances where energy intake actually limits lean growth? A coherent argument can be made that this situation does exist early in the pig's life and may continue well into the weanling period. Several experiments, cf. Cook et al., 1991; Nam and Aherne, 1994, have shown that rate of gain is increased by adding fat to the nursery diet. Cook et al. (1991) demonstrated that fat addition resulted in an absolute increase in daily caloric intake by pigs between weaning and 50 pounds live weight. Given that much of the total body weight gain in weanling pigs is protein mass, it is likely that increasing energy intake does augment daily lean gain.

Restricting Energy Intake

Feed restriction programs designed to reduce the rate of fat growth have been employed for decades in countries where the market rewards farmers for producing lean carcasses. Such programs are described in various publications (ARC, 1979; English et al., 1988). Automated feeding systems are often employed to facilitate feed-restriction.

It would seem logical that energy intake could be reduced by feeding low-energy or diluted diets. Unfortunately, the pig has a significant capability to increase the volume of feed consumed in order to maintain a fixed level of energy intake. The ability to over-eat appears to be a function of the dietary diluent that is used. In a classical experiment, Baker et al. (1968) found that pigs could over-eat to maintain energy intake even when the diet contained 40% sand. But, the addition of only 10% fiber (cellulose) resulted in a depression in daily energy consumption. In contrast, Kennelly and Aherne (1980) reported that finishing pigs fed diets containing 22% oat hulls were able to increase feed intake to maintain digestible energy intake.

We recently conducted an experiment to determine whether the percent lean in the carcass at slaughter could be increased by feeding a diet with a selected combination of diluents. The diet formulations are shown in table 4. Three diluents were used: wheat bran, corn gluten feed and

Table 4. Diet composition

	Diet Number				
Ingredients	1	2	3	4	5
Corn	68.65	75.95	62.70	49.45	36.15
Soybean meal	24.40	22.00	17.50	12.90	8.40
Fat	5.5	-	-	-	-
Wheat bran	-	-	10.00	20.00	30.00
Corn gluten feed	-	-	5.00	10.00	15.00
Alfalfa meal	-	-	3.00	6.00	9.00
Dicalcium phosphate	1.10	0.90	0.60	0.25	-
Limestone	-	0.80	0.85	1.05	1.10
Copper sulfate	0.05	0.05	0.05	0.05	0.05
Illini vitamin premix	0.10	0.10	0.10	0.10	0.10
Trace-mineral salt	0.20	0.20	0.20	0.20	0.20
Total	100.00	100.00	100.00	100.00	100.00
Energy, kcal/lb	1593	1501	1410	1321	1231

alfalfa meal. This ingredient combination was selected on the basis of observations on feed consumption by pigs feed diets formulated with these products.

The pigs were fed in an enclosed building on partially- slotted floors from approximately 120 lbs to 250 lbs liveweight. Pigs were housed in pen-groups of five animals. The growth phase of the experiment was ended and growth data summarized when the pigs assigned to the treatment with the most rapid growth reached 250 lbs. Lighter weight pigs were continued on treatment until average weight within a pen reached approximately 250 lbs. They were slaughtered and carcass data were collected at the University of Illinois Meat Laboratory. The results are presented in table 5.

Table 5. Growth performance and carcass characteristics of finishing Pigs fed diets varying in ingredient content and energy density

	Diet Number				
Criterion	1	2	3	4	5
Initial weight, lbs	68.65	75.95	62.70	49.45	36.15
Final weight, lbs	244.04	248.01	243.61	232.80	226.85
Slaughter weight, lbs	250.88	251.16	246.47	248.89	245.15
Avg. daily gain, lbs	2.25	2.28	2.21	2.05	1.92
Avg. daily feed intake, lbs	6.41	7.23	7.40	7.12	7.29
Energy intake, Mcal/day	10.17	10.83	10.41	9.36	8.93
Dressing percent	75.97	74.90	74.56	73.96	73.51
Tenth rib fat thickness, in	.85	.86	.78	.70	.69
Loin eye area, in^2	5.71	5.57	5.68	5.62	5.34
Percent carcass lean	50.78	50.42	51.72	52.32	52.00

Treatment 1 contained added fat and, as expected there was a reduction ($P<.05$) in feed intake compared to the other treatments. Pigs did not increase ($P>.10$) feed consumption as dietary energy declined. Dressing percentage was significantly affected by diet. As the inclusion levels of high fiber ingredients increased, dressing percentage decreased. Backfat thickness was significantly reduced by feeding the low-energy diets but loin eye size was not affected. Carcass lean percentage for pigs fed 1321 kcal/lb was greater ($P<.05$) than for pigs fed the control, corn-soybean meal diet, i.e., treatment 2.

The results of this experiment permit the suggestion that diet formulation can be used to alter the composition of pigs at slaughter. The reduction is fatness is accompanied by a reduction in average daily gain.

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FEEDING FOR MAXIMUM EARLY LEAN GROWTH

DON MAHAN

Summary

To achieve maximum lean growth, the young pig's feed sources must be adapted to the limitations of the digestive tract. Younger lighter weight pigs must be fed protein sources of high digestibility and amino acid availability. Young weanling swine may secrete inadequate quantities of hydrochloric acid and a source of organic acid or chloride will improve feed efficiencies. Energy in the form of simple carbohydrates is essential during the early period postweaning, but both carbohydrates and fats (oils) are important energy sources during the latter part of the starter period.

Introduction

Regardless of whether we raise our own pigs or buy feeder animals, it is essential that to achieve optimum and(or) maximum performance, the animal must get off to a good start. A pig less than 50 lbs. bodyweight, regardless of genotype, has a high priority for muscle formation, and the development of this tissue can be accentuated or hindered by several factors, not all of which are nutritional. Because lean growth is high in young animals and because pigs are being weaned earlier today than just a decade ago, this review will evaluate various nutritional aspects essential to achieve optimum lean tissue growth.

It has been long recognized that the three critical areas for weaning pigs at any age and(or) starting feeder pigs onto a grower-finisher program involves a control over 1) environment (including facilities), 2) disease, and 3) nutrition. The younger and(or) lighter the animal when the program is started, the more critical attention must be given to each area. Each of these areas can also be further subdivided and each must be critically assessed fitting known technologies into the management systems available. Although the principles are the same, the applications are different.

Weaning age is today undergoing a dramatic change in the swine industry with many producers adopting the earliest weaning program which will enhance the profitability of their enterprise. In some cases, this may involve weaning at 10 days of age; whereas in other situations conditions may not warrant such a program and weaning must occur later.

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Understanding Physiological Changes

Early weaning requires knowledge about the physiological changes the animal is undergoing and then to adapt this knowledge which will maximize the animal's growth opportunities. The area that requires a thorough understanding is the digestive capability of the animal at various ages and then to formulate diets which will minimize the physiological limitations of the weaned pig.

Digestive Enzymes. The digestive tract of the pig undergoes a dramatic adjustment upon weaning. Digestive conditions in the nursing animal utilizes a supply of nutrients which surpass digestibilities greater than 95%. Milk nutrients are easily broken down by the enzymes in the intestinal tract. Upon weaning, there is now introduced a combination of feed sources with digestibilities which range from 70 to 90%. Diets are generally provided on a dry basis and the protein component of several feedstuffs can stimulate adverse immune reactions in the digestive lining of the young animal particularly if their dietary level is too high. Feeds for the weanling pig contain larger more complex molecules than were present in milk which must subsequently be broken to component parts (i.e. nutrients) which are then absorbed and utilized to manufacture pig tissue. The digestive enzymes change dramatically to 8 weeks of age (Figure 1). Consequently, both weaning age and weaning weight become a critical determinant in what feeds can be digested and subsequently used in the diet. Pigs of a younger age and lighter body weight should be provided feeds which have a high digestibility; whereas, older pigs weaned at heavier weights can effectively utilize feeds which have a larger

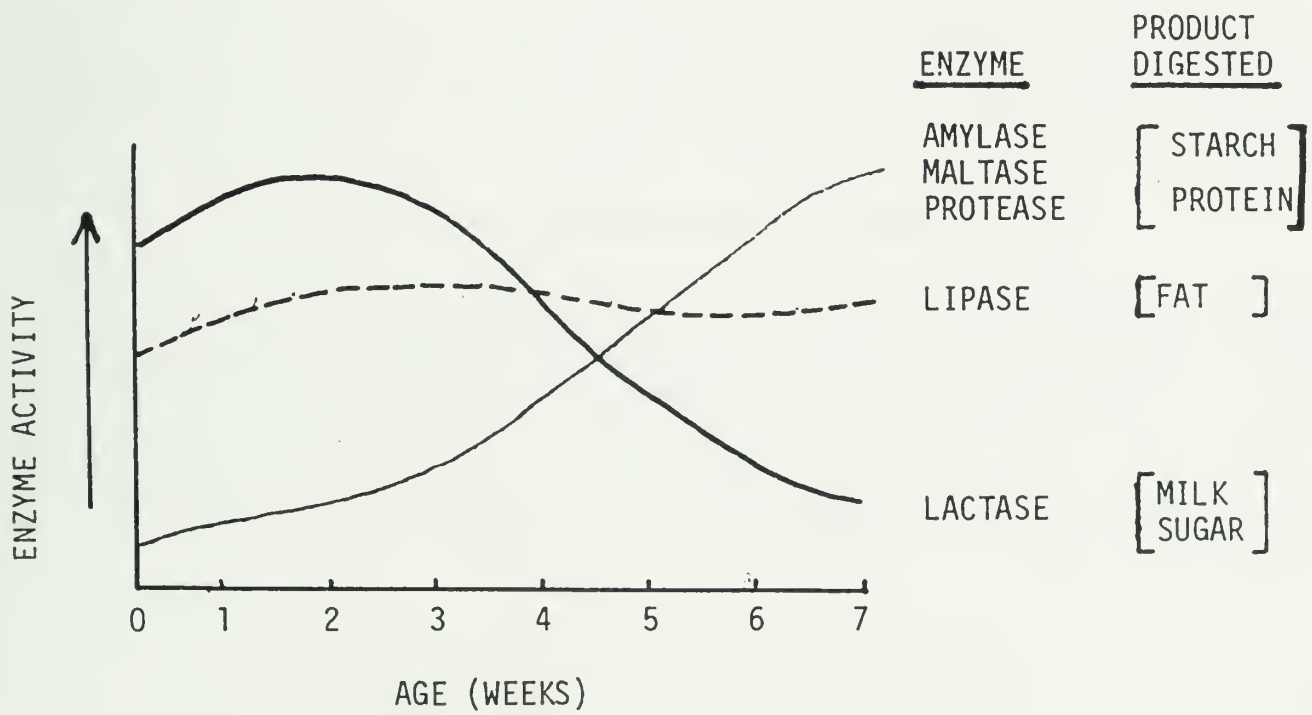

Figure 1. Digestive Enzyme Patterns in the Pig from Birth to 8 Weeks.

proportion of the cereal-vegetable products which are also cheaper. Feeds of a high acceptability generally are feeds of a high digestibility and should be provided during the initial phases postweaning. This concept has resulted in the current phase feeding program recommended today by feed companies and swine nutritionists. It must be emphasized that for pigs to digest feed it is first essential that they consume the diet. Consequently, feed intake is perhaps the most important determinant in how pigs respond not only during the initial week postweaning, but it may and probably will affect the pig's subsequent performance to market weight.

Intestinal Morphology. A second major obstacle to recognize is the change in the intestinal morphology which occurs upon weaning and the influence this change has on subsequent nutrient absorption. During the nursing period, the intestinal villi (the source of some digestive enzymes and the absorption site of nutrients) are long and very effective in the digestive and absorption process. Upon weaning, the villi become sloughed and(or) the surface area is dramatically reduced (Cera et al., 1988). Consequently, not only is a source of digestive enzymes eliminated (i.e. from the tips of the villi) but the absorption mechanism for nutrients is disturbed. Consequently, we must provide diets to younger pigs that contain feed components that are highly digestible, not antigenic to the intestinal lining and highly absorbable. The duration that these highly digestible diets should be fed depends largely upon economics, but the age and weight of the pig must also be taken into consideration. Younger and lighter weight pigs should be fed the more highly enriched diets for a longer time period.

The principle theme to be recognized is that when pigs are weaned early and (or) at a light body weight they must be protected against any factor which will arrest their growth potential. When the three areas (environment, disease, nutrition) are properly applied, we are not talking about a reduction in mortality, but in reality a reduction in morbidity (i.e. poor performance).

Maximizing Postweaning Pig Growth

Weaning Age and Weight. Regardless of weaning age, there is a wide range in pig weights which occur and this must be taken in to account when planning a nursery feeding program. Figure 2 presents the cumulative percentage of over 6000 pig weights collected at 21 d of age. The average weight at 21 days was 13.2 lb. It is of interest to note that 25% of the pig's weighed less than 11.0 lbs. at 21-days of age while 25% were heavier than 15.0 lbs. Clearly, we must recognize that the pig's ability to utilize nutrients at these weight extremes differs and they should be fed accordingly.

The effects of different weaning weights (constant age) and fed appropriate Phase I, II and III diets during the nursery period and then constant diets during the grower-finisher period to market weight is presented in Table 1. Even when the lighter weight pigs (9-11 lbs.) were fed the enriched high nutrient dense diet during the initial two weeks postweaning and compared to the performance responses of heavier weight (16-19 lbs.) weanling pigs, it still took the lighter weight pigs approximately two weeks longer to attain market weight. To evaluate whether this was simply a response of weaning weight or weaning age, another experiment was conducted

which evaluated whether light (9-12 lbs.) or heavier (15-18 lbs.) weight pigs allowed to nurse the sow for an additional week, would compensate for their lower initial weaning weights during the grower-finisher period. The results in Table 2 implies the benefit may result in allowing lighter weight pigs to nurse the sow for a longer time period. Whether this response was due to the superior composition and digestibility of the nutrients in sow milk or whether some other factor present in milk may affect later nutrient utilization is unclear. The results of Cera et al. (1988) and Simmen et al. (1990) suggest that there are indeed growth factors present in sow milk that can influence the maturation process of the intestinal tract of the pig which in turn may influence later nutrient absorption and utilization.

Table 1. Effect of Pig Weanling Weight on Performance Responses to Market

Item	**Weaning Weight, lb.**			
	9-11	**12-15**	**16-19**	**SEM**
No. Pigs	70	70	70	--
Weaning age, days	24	25	25	.6
Nursery Period				
Length (Phase I, II, III), wk	2+2+2	1+2+2	0+2+2	--
Daily gain, lb.	.86	.94	.88	.04
Daily feed, lb.	1.51	1.58	1.44	.06
Final weight, lb.	46.5	47.2	43.4	.88
Grower-Finisher (to 230 lb.)				
Daily gain, lb.	1.60	1.61	1.65	.04
Daily feed, lb.	5.07	5.14	5.05	.13
Days	114	113	111	3.5
Overall (Birth to 230 lb.)				
Days	180	172	165	3[a]

Source: Mahan and Lepine (1991).

[a]Linear response ($P < .05$).

Table 2. Effect of Pig Weight (23 Days) and Weaning Age (23 or 30 Days) on Performance Response to Market Weight

Item	Weight (23-d), lb. / Age at Weaning, d	9-12 / 23	9-12 / 30	15-18 / 23	15-18 / 30	SEM
No. Pigs		72	72	72	72	--
Weight, lb.						
23-d		10.6	10.6	17.5	17.5	.3[a]
30-d		13.2	14.5	20.9	22.6	.5[a]
Nursery						
Length, wk						
Phase I		2	1	1	0	--
Phase II		2	2	2	2	--
Phase III		2	2	2	2	--
Total, wk.		6	5	5	4	--
Final Weight, lb.		46.5	48.9	50.7	50.9	1.2[a]
Daily gain, lb.						
Nursery (to 45 lbs.)		.83	.91	.95	.95	.02[ab]
45 to 230 lb.		1.76	1.79	1.82	1.85	.04[ab]
Daily feed						
23 d to 230 lb.		4.28	4.27	4.53	4.53	.07[ab]
Birth to 230 lb., days		180	177	169	168	2[a]

Source: Mahan (1993).

[a]Initial Weight (23 d) response ($P < .05$).
[b]Weaning Age (23 vs. 30 d) response ($P < .05$).

The question often arises whether poor growth performances during the initial period postweaning will affect later performance or whether compensatory growth responses would occur during the later grower-finisher period to make up for initially lower weights or gains. The results presented in Tables 1 and 2 demonstrate no compensatory benefit in improved gain, feed intake, or days to market weight when pigs were of a lighter weaning weight. Data from Tokach (1992) and Toplis and Tibble (1995) presented in Tables 3 and 4, respectively demonstrated that when pigs gained at a lower rate during the initial week (Table 3) or weeks postweaning (Table 4), these pigs continued to have lower gains to market weight with little compensatory response. Although some research has shown some compensatory response to early dietary insults, it is clear that initial gains postweaning can be important in the pig's

subsequent performance to market. Gains postweaning generally reflect feed intake. Diets consumed in larger quantities result in larger pig gains.

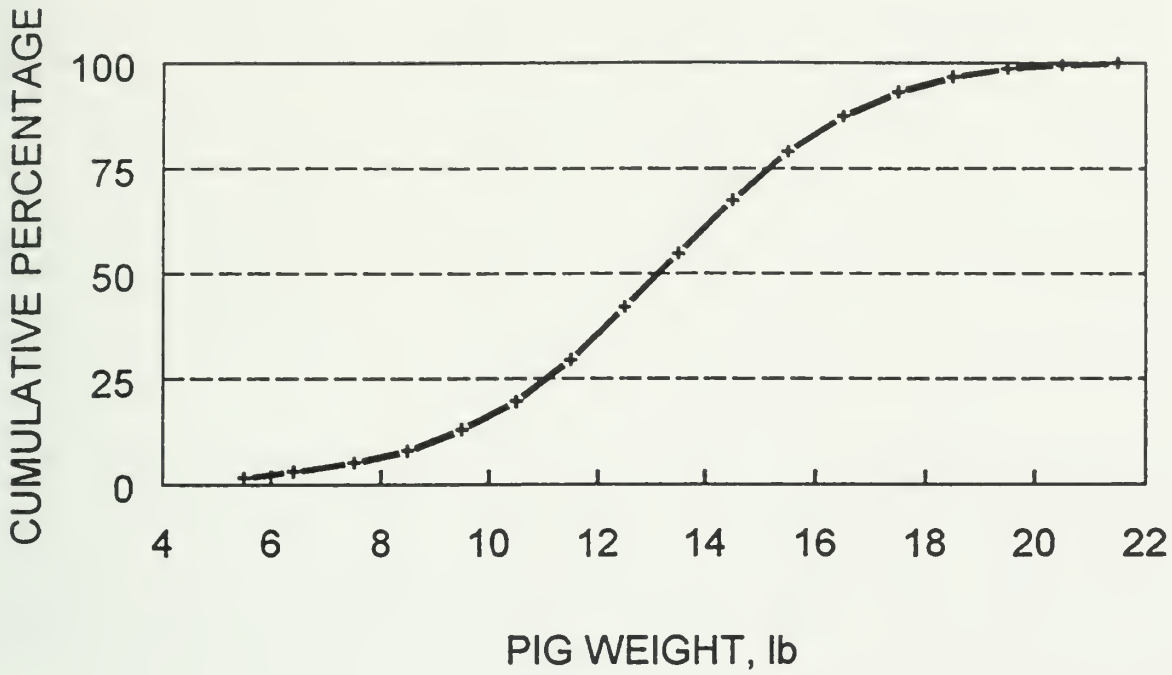

Figure 2. Cumulative Pig Weight Distribution (N = 6036 Pigs; 21 Days of Age)

Table 3. Effect of Daily Gains During the First Week Postweaning on Subsequent Pig Performance.

Period Postweaning	**Daily Gain (0-7 d), lb.**			
	0	**0-.33**	**.33-.50**	**>.50**
		Pig Weights		
28 day	32	35	37	40
56 day	66	68	72	77
156 day	232	239	246	250
Days to 250 lb.	183	179	175	173

[a]Source: Tokach et al. (1992).

Table 4. Effect of Initial 14-Day Postweaning Daily Gain Responses on Subsequent Pig Performance.

Item	Weaning Age, d Weight, lb.	24 13.2	24 13.2	24 13.2	24 13.2
Performance (0-14 d)					
Daily gain, lb.		.72	.64	.49	.33
Weight, lb.		23.4	22.3	20.1	17.9
Daily gain to 70 d, lb.		1.44	1.29	1.00	.86
Daily gain to 200 d, lb.		1.93	1.70	1.41	1.28
Total Days		120	133	155	170

Source: Toplis and Tibble (1995).

Dietary Protein Sources. Because growth rate postweaning appears to be critical, it is essential that the pig be provided diets of adequate nutrient content with feeds that the pig can effectively utilize for each production phase. Table 5 lists the major protein sources commonly used in the diets of pigs during the various phases postweaning and the dietary levels usually used in formulation practices. Although this table implies that the list is more extensive for SEW and Phase I feeding programs, the reason they are reduced or eliminated from the diets of later productions phases is due to their high cost. Consequently, in order to maximize lean tissue growth and to do so economically, the nutritional level should be adequate with it's digestibility high enough to meet the pig's amino acid requirements. Table 6 uses available body composition data and estimates for dietary lysine requirement of pigs during Phase I, II, and III of the nursery period.

Table 5. Protein Source Commonly Used in Diet Formulation During Various Phases Postweaning.

	Dietary Level of Ingredient (%)			
Protein Source	**SEW**	**Phase I**	**Phase II**	**Phase III**
Soybean Meal	10-12	10-15	15-20	20-25
Soy Protein Conc.	5-10	5-10	2-5	0
Dried Whey	20-30	15-25	15-25	15-25
Whey Protein Conc.	10-15	5-15	0-10	0-5
Porcine Plasma	8-10	5-10	0	0
SD Blood Protein	2-4	2-4	1-2	0
Fishmeal	0-5	0-5	0-5	0-5
Potato Proteins	3-5	3-5	0-5	0

Table 6. Predicted Lysine Requirement of Weanling Pigs During Different Production Phase

Item	Phase I	Phase II	Phase III
Weight gain, lb/d	.55	1.15	1.40
, g/d	250	525	640
Protein deposition, g/d[a]	40	84	102.4
Lysine deposited, g/d[a]	3.2	6.7	8.2
Feed conversion	1.1	1.25	1.40
Dietary Lysine level, %[b]	1.45	1.30	1.20

[a]Source: Shields (unpublished data); assumes a protein gain of 16.0% of weight gain and a content of 8.0% lysine.

[b]Assumes an apparent digestibility of 80%.

Dietary Energy Sources. If the pig is weaned early, it can lose a substantial amount of body fat content within a short time postweaning, whereas, pigs weaned at a later age will not demonstrate this body fat loss (Figure 3). Consequently, energy has often been neglected and is perhaps a major limiting nutritional factor for the weanling pig. An adequate level of energy must be supplied to the young pig to prevent body fat loss postweaning, but the form of energy is critical.

Adding fat (oil) to the diets of young pigs during the initial two weeks postweaning has generally not resulted in improved gains, nor has it influenced feed intake, but there has been some benefit in improved feed efficiency (Table 7). However, when the energy source is in the form of a simple carbohydrate (i.e. lactose, dextrin) resulting pig gains are improved when dietary levels of simple carbohydrates are between at 25 to 30% (Table 6). Although this experiment used lactose as the simple carbohydrate, there are other carbohydrate sources just as effective.

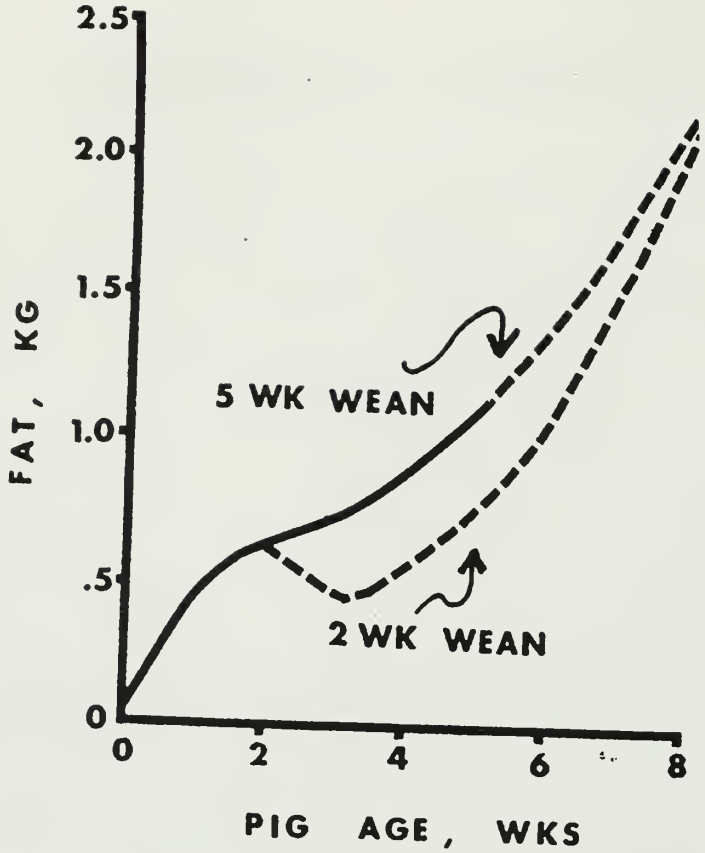

Figure 3. Body Fat Changes in Pigs Weaned at Two Ages.

After the initial two week period, there continues to be a positive influence on pig gains from the addition of simple carbohydrates in the diets of weanling pigs (Table 7), but fat begins to have a more prominent role. Daily gains and feed intakes were improved when the diet contained a simple carbohydrate levels of approximately 20%. When soybean oil was added at a 5% level, gains and feed efficiencies were improved ($P < .01$) with a concurrent reduction in feed intake. There was no interaction between these two energy sources. These results suggest that during the transition period postweaning dietary fat is more difficult to utilize by the weanling pig with the major source of energy most effectively utilized by the young pig being carbohydrate, whereas during the latter part of the starter period, both forms of energy result in beneficial responses. The carbohydrate source must not, however, be of a complex (i.e. starch) nature. The digestive enzymes of the young pig do not appear adequate to hydrolyze the starch of corn.

Table 7. Effect of Dietary Simple Carbohydrate (Lactose) and Dietary Oil (Soybean Oil) on Postweaning Performance Responses.

Item	Lactose, %			Soybean Oil, %		SEM
	0	20	40	0	5	
No. Pigs	86	86	86	176	176	
0-14 Day[a]						
Daily gain, lb.	.58	.68	.64	.62	.62	.02[b]
Feed intake, lb.	.88	.94	.93	.93	.91	.02[b]
Gain:Feed	.66	.71	.69	.66	.72	.01[bc]
14-35 Day[d]						
Daily gain, lb.	1.19	1.26	1.22	1.19	1.26	.02[bc]
Feed intake, lb.	1.94	2.11	1.91	2.04	1.93	.03[bc]
Gain:Feed	.68	.60	.64	.58	.65	.01[bc]

[a]Dietary lysine level was 1.40%.
[b]Lactose response ($P < .01$).
[c]Soybean oil response ($P < .01$).
[d]Dietary lysine level was 1.30%.

Diet Acidification. Research conducted at Illinois demonstrated that organic acids when added to the diets of weanling pigs have resulted in improved gains and feed efficiencies (Table 8). Giesting et al. (1991) demonstrated that corn soybean meal diets with 3% fumaric acid improved pig performance responses throughout a four week postweaning period, but the greatest response was during the initial two weeks postweaning. When milk products were used in the diets, a similar response was obtained, but not of the magnitude when the cereal grain-diet was fed. The young pig does not secrete large amounts of hydrochloric acid from birth to weaning and it is thought that organic acids help to activate the enzymes (i.e. pepsinogen) involved in protein digestion and (or) to curtail the growth of bacteria in the stomach or intestinal lumen.

Table 8. Effect of Diet Acidification with an Organic Acid on Pigs Fed Different Types of Diets.

Item Fumaric Acid, %:	C-SBM 0	C-SBM 2	C-SBM 3	C-SBM + DSM (25%) 0	C-SBM + DSM (25%) 2	C-SBM + DSM (25%) 3	SEM
0-2 wk							
Daily gain, lb.	.29	.33	.38	.43	.49	.43	.05[a]
Daily feed, lb.	.67	.65	.67	.69	.73	.68	.05
Gain:Feed	.43	.51	.56	.60	.67	.63	.05[ab]
0-4 wk							
Daily gain, lb.	.64	.71	.69	.72	.79	.77	.05[a]
Daily feed, lb.	1.19	1.21	1.18	1.17	1.25	1.18	.07
Gain:feed	.54	.58	.58	.61	.64	.65	.01[ab]

Source: Giesting et al. (1991).
[a]Dried Skim Milk (DSM) response ($P < .05$).
[b]Fumaric acid response ($P < .01$).

It has also been demonstrated that various milk products and vegetable proteins can act as buffers in the stomach which effectively binds available hydrochloric acid secreted in the stomach, which ultimately reduces the digestibility of dietary protein. Because many protein sources used in SEW and Phase I starter diets have a high acid buffering capacity (Table 9), it was perhaps not surprising that organic acids added to these diets would be beneficial in the diets of young pigs.

Dried whey is inherently high in it's ash content (> 8.0%) and has a high sodium content (> 1.0%). When salt was added to a corn soybean meal dry whey diet, there was a growth response during the initial 14 days postweaning and a corresponding increase in feed efficiency (Table 10). Subsequent research demonstrated that the majority of this response was attributed to the chloride content of the salt where pig gains, feed intakes and feed efficiency were all improved when chloride was added to the diets (Table 11). The addition of salt or chloride during the latter postweaning period did not result in a positive growth response (Tables 10 and 11).

Table 9. Acid Binding Capacity (ABC) of Feed Ingredients Used in Starter Pig Diets.

Feedstuff	ABC (pH 4.0)[a]
Wheat	6.2
Corn	8.0
Soybean meal, 44%	41.7
Soy Protein Concentrate	50.0
Dried Whey	48.5
Porcine Plasma - 820	126.1
Porcine Plasma - 920	93.8
Fishmeal	52.1

[a]The quantity of HCl (mMole) necessary to bring a 100 g sample to a pH 4.0.

Porcine plasma has been shown to enhance pig gains dramatically during the Phase I period postweaning. This product, however, is also high in sodium, chloride, and in it's acid binding capacity (Table 9). The results of an experiment where salt (NaCl) was added to Phase I diets containing 6.5% plasma protein resulted in a linear growth and feed efficiency response (Table 12). Again, this response was attributed to the chloride component where in a second experiment, it's addition resulted in improved pig gains and feed efficiencies (Table 13). Other work has demonstrated that hydrochloric acid production in the pig also declines postweaning. When feeds are fed that have a high acid buffering capacity (i.e. vegetable proteins, porcine plasma, milk proteins), the young pig's potential ability to digest these protein feeds is reduced. Consequently, the addition of chloride to the diets of early weaned pigs has subsequently been shown to enhance feed efficiency. This suggests that the protein digestibility in the young weanling pig may be limiting the pig's lean growth and the addition of added salt (NaCl) or another source of chloride would benefit the young pig until hydrochloric acid secretion increases with age. Consequently, the value of added chloride to these diets was shown to diminish as the pig ages and as stomach HCl production increases.

Table 10. Effect of supplemental sodium chloride to corn-soybean meal-dried whey diets for weanling pigs.

		NaCl level, %				
		0[b]	.20	.40	.60	
	Total Na, %:	.20	.32	.44	.56	
Item[a]	Total Cl, %:	.35	.43	.51	.59	SEM
Daily gain, lb.						
0 to 7 d		.16	.20	.24	.26	.01[c]
8 to 14 d		.56	.61	.64	.62	.02[d]
0 to 14 d		.36	.40	.44	.44	.01[e]
15 to 35 d		1.17	1.17	1.20	1.16	.03
Daily feed intake, g						
0 to 7 d		.47	.43	.45	.48	.02
8 to 14 d		.94	.88	.93	.94	.02
0 to 14 d		.71	.66	.69	.71	.02
15 to 35 d		2.05	2.04	2.01	2.09	.04
Gain:feed ratio						
0 to 14 d		.53	.61	.64	.62	.03[d]
15 to 35 d		.57	.57	.60	.55	.01

[a]Fourteen replicates were conducted (84 pigs/treatment group). Pigs were weaned at 23 ± 2 d of age and averaged 6.63 kg BW.

[b]Chemical analysis of the basal diet (as fed basis) averaged .20% Na, 1.35% K, and .35% Cl.

[c]Linear response ($P < .01$).

[d]Quadratic response ($P < .08$).

[e]Linear response ($P < .05$).

Table 11. Effect of supplemental hydrochloric acid to corn-soybean meal-dried whey diets for weanling pigs.

		Added Cl, %[b]			
		0	.05	.10	
Item	**Total Cl, %**	**.40[c]**	**.45**	**.50**	**SEM**
Daily gain, lb.					
0 to 7 d		.17	.23	.28	.03[d]
8 to 14 d		.61	.63	.68	.02[e]
0 to 14 d		.39	.43	.48	.02[d]
15 to 35 d		1.20	1.24	1.17	.04
Daily feed intake, lb.					
0 to 7 d		.40	.41	.47	.04[e]
8 to 14 d		.85	.87	.99	.05[f]
0 to 14 d		.62	.64	.73	.04[e]
15 to 35 d		1.97	1.96	1.83	.06
Gain:feed ratio					
0 to 7 d		.44	.56	.60	.04[e]
8 to 14 d		.71	.72	.75	.03
0 to 14 d		.62	.67	.65	.03
15 to 35 d		.61	.63	.64	.01

[a]Seven replicates were conducted (42 pigs/treatment group).

[b]Hydrochloric acid was added to the diets at various levels to provide the supplemental level of Cl.

[c]Chemical analysis of the basal diet (as fed basis) was: .20% Na, 1.25% K and .40% Cl.

[d]Linear response ($P < .01$).

[e]Linear response ($P < .08$).

[f]Linear response ($P < .05$).

Table 12. Effect of Added Salt (NaCl) to Phase I Diets Containing Porcine Plasma

Item	Added NaCl 0	.20	.40	.60	SEM
No. Pigs					
Daily gain, lb.					
0-7 day	.37	.41	.47	.46	.03
7-14 day	.73	.83	.91	.91	.04
Gain:Feed					
0-14 day	.59	.69	.72	.72	.02

Source: Mahan (unpublished data).

[a]Linear response (P < .05).

Table 13. Effect of Added Hydrochloric Acid to Phase I Diets Containing Porcine Plasma (6.5%).

Item	Added Cl 0	.10	.20	.38	SEM
Daily gain					
0-7 day	.33	.38	.36	.38	.02[a]
7-14 day	.59	.68	.70	.76	.03[a]
Gain:Feed					
0-14 day	.62	.67	.66	.70	.04[a]

Source: Mahan (unpublished data).

[a]Basal diet contained .08% Cl, .20% Na and .68% K.

[b]Linear response (P < .05).

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THE ROLE OF BETAINE AND CARNITINE IN LEAN GROWTH MODULATION OF SWINE

JACK ODLE

Introduction

Within the last decade, escalating concerns among health-conscious consumers toward cholesterol (and red-meat consumption) have heightened the incentive for the swine industry to amplify its efforts to produce and market lean meat. Virtually all sectors of the industry have responded to the challenge. Breeding companies have worked through traditional genetic selection to improve carcass leanness, and using molecular techniques, are now working to identify markers to potentially accelerate the process. Growth biologists have investigated growth modulators such as β-adrenergic agonists and porcine somatotropin with great success. Packers have implemented sophisticated ultrasound technology to estimate carcass leanness and offer financial incentives for superior carcasses. Retailers have developed new products to appeal better to consumer demands for lean pork.

Nutritionists are also refining swine feeding programs to support maximal lean accretion. For example, the NRC is devising a modeling approach for estimating amino acid requirements which employs the lean growth potential of the animal as a driving feature of the model (Pettigrew, 1995). In addition, nutritional agents with alleged effects on carcass composition have also emerged in recent years. This presentation will examine the role that two such agents, betaine and carnitine, may have in modifying the growth process in swine. Specifically, the established metabolic roles of betaine and carnitine will be reviewed and will be followed by a summary of several swine growth trials in which betaine and carnitine have been fed.

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This manuscript has also been published as part of the 1995 Carolina Swine Nutrition Conference, Sheraton Imperial Hotel, Research Triangle Park, Raleigh, NC., November 7, 1995.

Structures, Physical Characteristics and Historical Background

As shown in **Figure 1**, betaine (also known as trimethyl glycine) and carnitine (3-hydroxy-4-trimethyl ammonium butyrate) have common structural features which include a carboxyl group at one end and a tri-methylated quaternary ammonium group with a fixed positive charge at the other. In addition, carnitine contains a hydroxyl group which serves as the site of fatty acid esterification (described later). The hydroxyl group of carnitine is attached to a chiral carbon such that carnitine is an optically active molecule, with the "L" form being biologically active. Betaine and carnitine have molecular weights of 117 and 161 respectively, are heat stable up to 200°C, and because of their charged and polar functional groups, both are highly water soluble and even hygroscopic. Betaine is widely distributed in the both plant and animal tissues; whereas, L-carnitine is found almost exclusively in animal tissues (name is derived from *carnis* meaning meat).

Both compounds are commercially available as internal salts -- betaine is available as a byproduct of sugar production from beets, and L-carnitine, historically purified from horse muscle, is now available in highly-pure form via stereospecific chemical synthesis.

Betaine has historically been marketed as a replacement for choline and methionine in broiler diets owing to it's metabolic role as a methyl donor (described in more detail later). Previous research with avian species has documented the ability of betaine to partially replace methionine (Pesti et al., 1979) or choline (Lowry et al., 1987) in diets that are marginal in methionine and choline respectively. The data indicate that betaine can spare a portion of the methionine and choline requirements that are specific to the need for labile

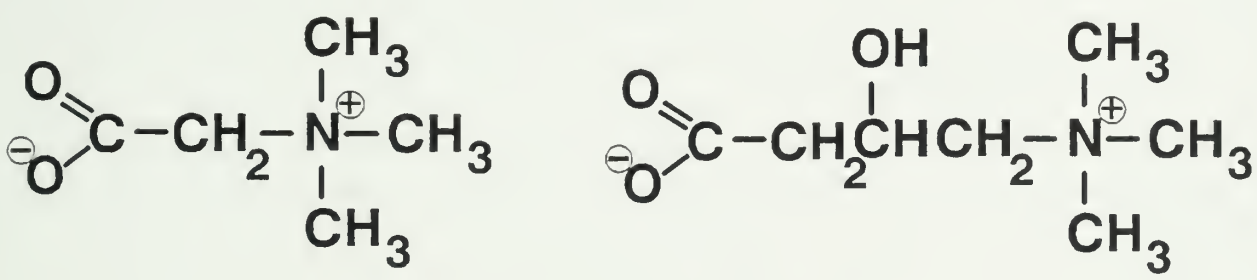

Figure 1. Chemical structures of betaine and L-carnitine showing their similar structural features. Carnitine is optically active whereas betaine is not.

methyl groups only. Thus, in practical avian diets (in which choline is only marginally low), responses to supplemental betaine and choline are similar. More recent research with broilers (Saunderson and MacKinlay, 1990) reported that betaine supplementation reduced carcass fat content compared to control diets. This was the first research to suggest effects of betaine supplementation on carcass composition and has led to subsequent research with swine that will be reviewed herein.

Academic research with carnitine has been conducted since the early 1950's when researchers at the University of Illinois found it to be an essential growth factor for the yellow meal worm (*Tenebrio molitor*) and thus named it "vitamin B_T" (Carter et al., 1952). While it is known that carnitine serves a metabolic role in the transport of fatty acids across the inner mitochondrial membrane for subsequent oxidation within the mitochondrial matrix (described in more detail later), higher organisms are able to synthesis sufficient amounts to meet the metabolic needs. Neonates may not be able to synthesis sufficient amounts, and thus L-carnitine is currently supplemented in soy-based formulas for infants. In addition, carnitine has been used within the medical community for the treatment of various organic acidemias and acidurias associated with metabolic disorders. Carnitine also has been marketed as and aid to human athletic performance. Only recently has carnitine's role in animal agriculture, and specifically swine production, been investigated.

Role of Betaine in Animal Metabolism

Methyl Donor

As a product of choline oxidation, it is well established that betaine serves as a source of labile methyl groups (i.e., 1-C units) in animal metabolism (**Figure 2**). Betaine is not the only source in that 1-C units are derived also from glucose via the β-carbon of serine, the 2-C of histidine, choline, the α-carbon of glycine, and the S-methyl carbon of methionine. The 1-C units are transferred to recipient molecules via S-adenosylmethionine (SAM), vitamin B_{12}, or via the folate 1-C pool and are vital to the synthesis of many compounds, including purine and pyrimidine bases of nucleic acids, trimethyl-lysine and carnitine (shown later, cf. figure 3), creatine, methylselenide, epinephrine, methyl-nicotinamide, choline, methylated DNA, etc.

The enzyme *betaine-homocystine methyl transferase* catalyzes the transfer of a methyl group from betaine to homocystine, producing methionine and dimethyl-glycine. Additional methyl groups from dimethyl- and monomethyl glycine are subsequently transferred into the folate-bound 1-C pool and can be used for nucleic acid biosynthesis, or may be transferred to homocystine by the B_{12}-dependant enzyme, *methyltetrahydrofolate-homocystine methyl tranferase* to yield methionine.

Clinical manifestations of derangements in 1-C metabolism vary depending on the cause, but include impaired feed intake and growth, fatty liver, anemia and infertility. Quantitatively, relatively large amounts of 1-C are needed in the form of phosphatidylcholine for membrane

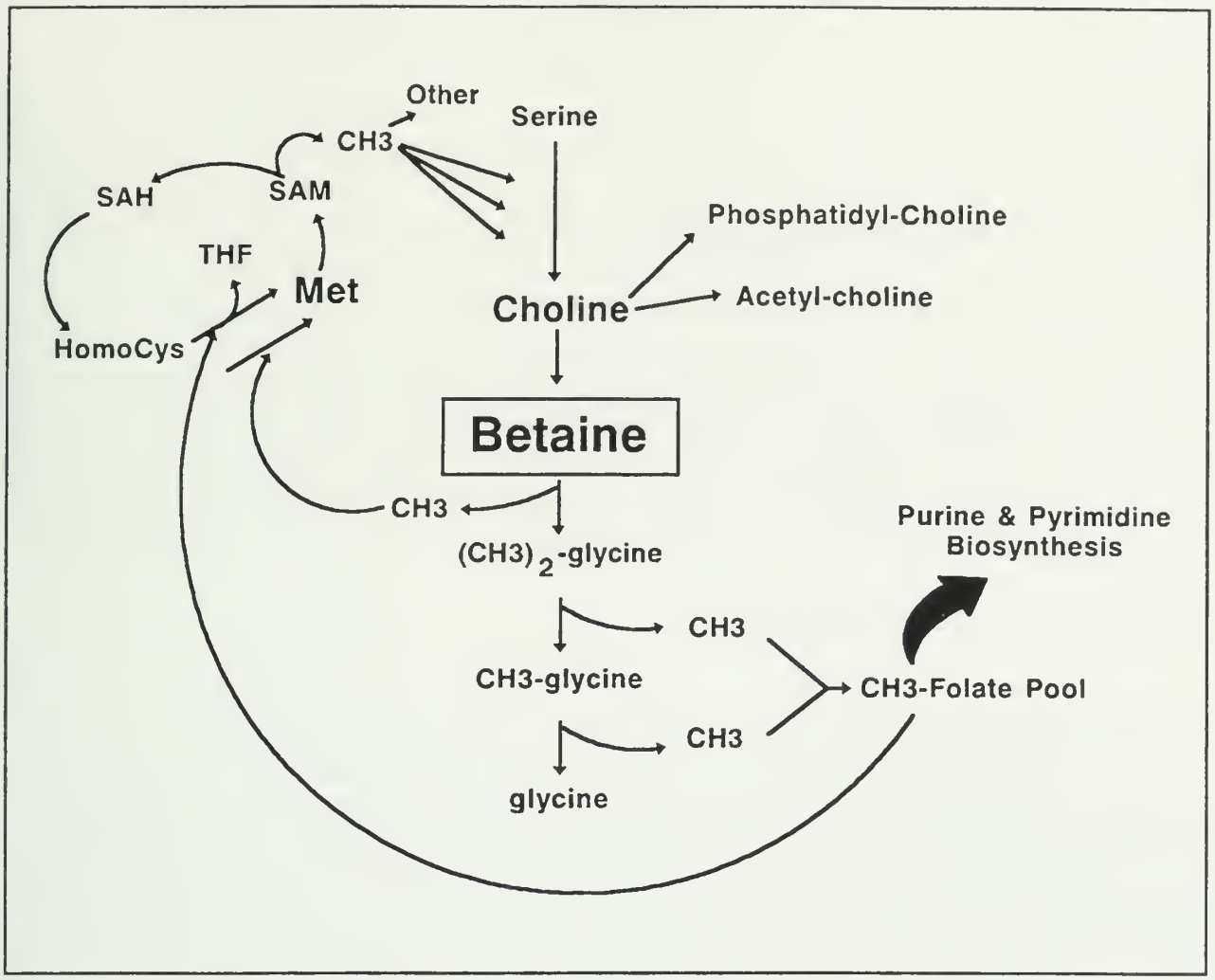

Figure 2. Metabolic role of betaine as a methyl-donor. Relationships between betaine, choline, methionine (MET) and folate (THF) are shown. SAM & SAH, S-adenosyl- methionine & homocystine respectively.

and lipoprotein biosynthesis, and thus, reduced growth and fatty liver ensue when 1-C units (choline) are deficient. When nucleic acid biosynthesis is impaired (e.g., during B_{12} or folate deficiency), rapidly dividing cells, such as hematopoietic and embryonic cells, are most susceptible and thus anemia and infertility can result. The latter has been exploited in the development of the anti-folate cancer drugs (e.g., methotrexate) which target rapidly dividing cancer cells.

Despite the important role of 1-C metabolism to the animal, betaine and choline are not generally considered essential dietary ingredients for swine fed corn-soy diets. Indeed, growing pigs fed typical corn-soybean meal diets do not respond to supplemental choline (NCR-42, 1980). However, a notable exception exists with pregnant swine in that improvements in reproductive performance were observed when practical corn-soybean meal diets were supplemented choline (NCR-42, 1976). This may be related to the increased 1-C needs for rapidly dividing embryonic cells. Similar observations have been made in human

studies (see Ziesel and Blusztajn, 1994 for review), and related research has implicated folate deficiency as a contributing cause of neutral tube defects (Czeizel and Dudas, 1992). Furthermore, methotrexate is being developed as an effective abortifacient.

Osmoprotectant

Normal cellular tonicity is maintained by a dynamic equilibrium of osmotically active molecules across semi-permeable cell membranes. Beyond the common inorganic electrolytes, betaine ranks among the important organic osmolytes (Petronini et al., 1992) which include sorbitol, inositol, and glycerolphophorylcholine, etc. (Bagnasco et al., 1986). Research with plants, bacteria and salmon (Yancey et al., 1982; Imhoff and Rodriguez-Valera, 1984; Chambers and Kunin, 1987; Virtanen et al., 1989) have suggested an important role of betaine as an osmoprotectant for cells exposed to osmotic stress. The efficacy of betaine as an osmoregulator in swine, however has not been demonstrated to date.

Role of Carnitine in Animal Metabolism

Synthesis From Protein-Bound Lysine

Carnitine is not considered to be a dietary essential nutrient for healthy adult mammals because sufficient quantities can be synthesized *de novo*. **Figure 3** illustrates the metabolic pathway of synthesis. The carbon "backbone" and nitrogen are derived from lysine, and the methyl groups are derived from S-adenosylmethionine (SAM; c.f. figure 2). It is important to note that free lysine is not subject to methylation, but rather, lysine contained in body proteins is the substrate for *SAM-dependent methytransferases* which produce peptide-bound

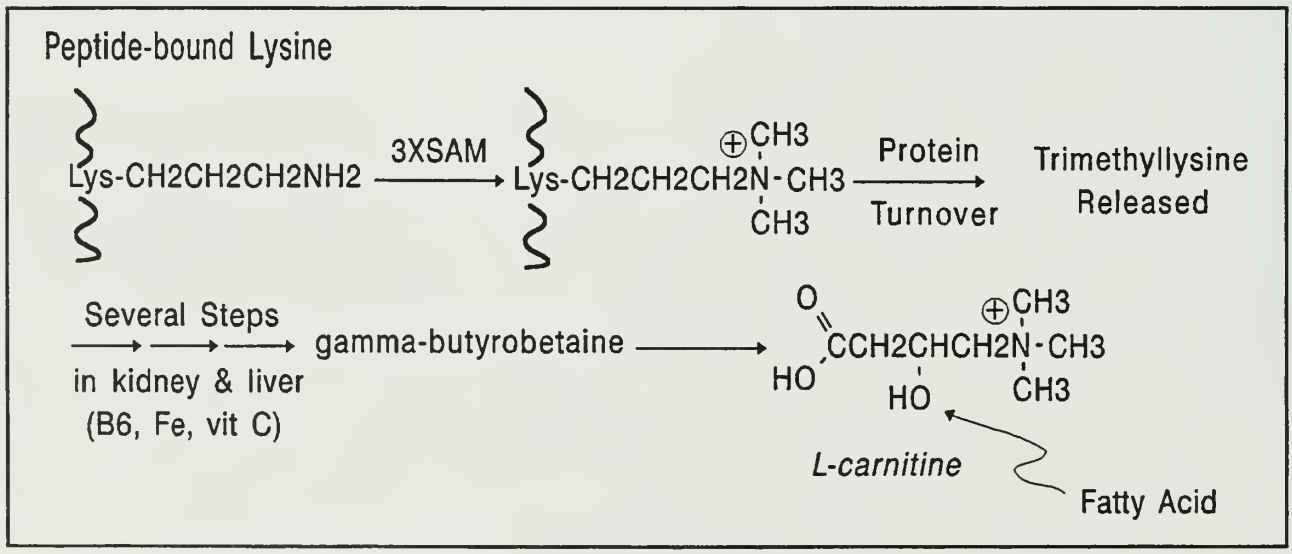

Figure 3. Abbreviated pathway of carnitine biosynthesis from protein-bound lysine, using methyl groups from S-adenosylmethionine (SAM).

trimethyl-lysine. The methylation step occurs in all tissues. When the methylated protein is degraded within the cell lysosome, trimethyl-lysine is released. Because trimethy-lysine cannot be re-incorporated into body protein, it enters the bloodstream and is either excreted, or is further metabolized by enzymes within the kidney and liver to produce L-carnitine. The last step adds the hydroxyl group to which the carboxyl-carbon of various organic acids (including fatty acids) may esterify. Thus, the carnitine synthetic pathway can be considered a "salvage" pathway of lysine degradation. Unlike betaine, carnitine cannot be degraded by mammalian enzymes, but is excreted in the urine as free carnitine or as short-chain carnitine esters (primarily as acetyl-carnitine).

The capacity of swine to synthesize carnitine has not been directly examined; however, plasma and tissue levels of carnitine are reduced in neonatal piglets reared on formulas devoid of carnitine (Baltzell et al., 1987). In addition, octanoate oxidation by colostrum-deprived piglets may be increased by L-carnitine supplementation (Kempen and Odle, 1993, 1995). These data parallel data from human infants, suggesting that carnitine may be a conditionally-essential nutrient for the neonate owing to reduced biosnythetic capacity.

Mitochondrial Transport of Fatty Acids

The major metabolic pathways of fatty acid metabolism are summarized schematically in **Figure 4**. Ancillary pathways of β- and ω-oxidation occurring in peroxisomes and endoplasmic reticulum, respectively, are not illustrated. In general, biosynthetic pathways are present in the cytosol, whereas oxidation occurs within the mitochondrial matrix. This subcellular compartmentation is central to the regulation and partitioning of fatty acid carbon flux between biosynthetic and oxidative fates within the cell, and carnitine plays a central role.

Long-chain fatty acids are first activated to their CoA thioesters via *synthetases* located in the endoplasmic reticulum and in the outer membrane of the mitochondria. The fatty acyl-CoA (FA-CoA) may then be esterified via *acyl-CoA transferases* (also located in the endoplasmic reticulum), forming various triglycerides, cholesterol esters, phospholipids, etc., which may be exported (from liver) as lipoproteins (VLDL) and stored in adipose tissue. The FA-CoA may alternatively be transported into the mitochondria via the coordinated activities of three carnitine-dependent membrane proteins (abbreviated collectively as CAT in figure 4): *carnitine acyltransferase* I catalyzing the formation of FA-carnitine from FA-CoA outside of the mitochondrial matrix, *translocase* catalyzing the exchange-diffusion (antiport) of FA-carnitine for free carnitine across the inner mitochondrial membrane, and *carnitine acyltransferase* II (CAT II), similar to CAT I except residing on the matrix side of the membrane.

The CAT I and II activities are catalyzed by a family of acyltransferase enzymes. Specifically, proteins have been identified with optimum activity toward C2, C8 and C16 FA-CoAs in various tissues and subcellular organelles. These are the only mammalian enzymes known to utilize carnitine. Within the mitochondrial matrix, the FA-CoA are subjected to oxidation at the β-carbon yielding acetyl-CoA which may be further oxidized to

CO_2 in the TCA cycle. Alternatively, the acetyl-CoA may exit as acetyl-carnitine (using the CAT system in reverse) or may produce ketone bodies (in liver tissue).

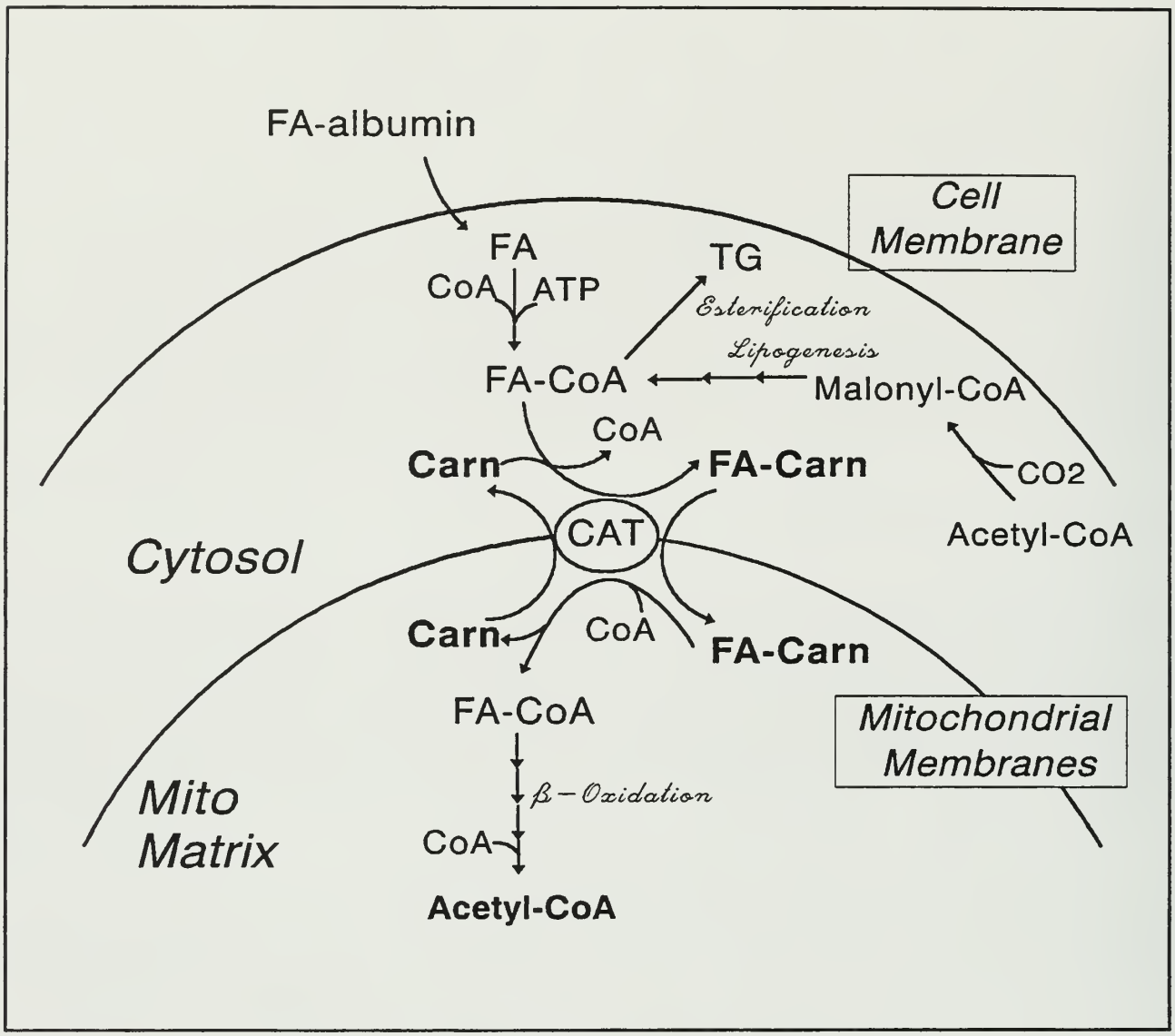

Figure 4. Role of carnitine (CARN) in transport of fatty acids (FA) into mitochondria, via carnitine acyltransferase (CAT), for oxidation. Note that lipogenesis occurs in the cytosol.

Thus the primary metabolic role for carnitine is as a cofactor for enzymes which shuttle long-chain fatty acids across the otherwise impermeable inner membrane of the mitochondria. Because of the heavy reliance of muscle tissue on the use of fat as an oxidative fuel, it is not surprising that skeletal muscle contains up to 90% of the total carnitine in the body. It also has been suggested that carnitine may play a role in "buffering" the acyl-CoA to free-CoA ratio in the cell which may be of particular importance during accelerated fatty acid oxidation (Kempen and Odle, 1993, 1995) and in patients with various metabolic disorders in which atypical CoA esters may accumulate.

Results of Swine Feeding Studies

Betaine

Considerable research has been conducted investigating betaine supplementation (at .1 to .2%) in swine diets, focused particularly on the finishing phase and effects on carcass characteristics. This focus was spawned by initial studies (Cadogan et al., 1993), which reported a 14.8% reduction in backfat of gilts fed .125% betaine for 35 days prior to slaughter. Despite the extensive number of follow-up trials that have been conducted, no research has been published in peer-reviewed journals. Consequently, important

Table 1. Summary of seven U.S. field trials involving betaine supplementation for late finishing pigs on changes in backfat (BF) and carcass yield†

Trial	No. Pigs/Treatment		Genetics	Sex*	Packer	%BF Decrease vs Control	% Yield Change vs Control
	Control	Betaine					
A	80 90	98 90	PIC PIC	B G	IBP IBP	7.1 2.7	0.65 0.52
B	370	124	PIC	M	Monfort	14.6	2.00
C	273	273	?	M	Frmland	7.9	0.97
D	127	124	?	M	Hormel	5.5	0.40
E	42	39	GIS	M	Excel	13.0	-0.27
F	37	38	?	M	IPC	13.6	0.00
G	603	100	F.Hybrid	M	Hormel	18.9	1.02
Total	**1622**	**886**				**12.0%**	**1.01%**

* B = barrows, G = gilts, M =mixed sex.
†, Adapted (with permission) from Shurson et al., 1994.

experimental details (e.g., choline and methionine levels, etc.) are often unavailable which precludes detailed comparisons of existing data. None-the-less, summarizing several early field studies (**Table 1**), Shurson et al. (1994) concluded that the inclusion of betaine for more than 30 days prior to slaughter could, in most cases, produce positive carcass benefits (reduced backfat and increased yield).

Since then, several additional trials have been completed and published in abstract form (**Table 2**). In addition to main effects of betaine supplementation, these studies also examined interactions with sex (Cera and Schinckel, 1995; Haydon et al., 1995; Webel et al., 1995; Lawrence et al., 1995) genotype (Cera and Schinckel, 1995; Webel et al., 1995) feeding duration (Cera and Schinckel, 1995) and other nutrients (i.e., choline, methionine and lysine; Smith et al., 1995; Campbell et al., 1995; Lawrence et al., 1995; Haydon et al., 1995). Due to the varied nature of the experimental designs and the results obtained from these studies, it is difficult to draw general conclusions.

In contrast to the previous field studies (Table 1), six out of the eight studies (Table 2) failed to detect effects on carcass backfat; however, several reported modest and inconsistent positive effects on loin measurements or growth-performance parameters. Nearly all studies examining sex effects noted betaine-by-sex interactions. Betaine supplementation decreased intake (Cera and Schinckel, 1995; Haydon et al., 1995) and improved feed efficiency (Cera and Schinckel, 1995) in gilts more than barrows (or intact males); whereas, betaine tended to increase daily gain (Webel et al., 1995) and decrease backfat (Lawrence et al., 1995) in barrows more than gilts. On the other hand, interactions with genotype were undetectable (Cera et al., 1995; Webel et al., 1994, 1995). Interactions with dietary lysine also have been variable in that betaine increased daily gain when fed to pigs receiving high (0.85%) lysine compared with 0.70% (Lawrence et al., 1995), but Haydon et al. (1995) reported positive betaine effects only when low lysine:calorie diets were fed. And finally, Campbell et al. (1995) reported that when a methionine-deficient (0.19% met+cys) basal diet was supplemented with betaine (0.125%), feed efficiency was improved to the same degree as when methionine was supplemented (to 0.23%).

In summary, initial field trials have suggested that betaine supplementation to swine diets during the finishing phase may improve carcass characteristics, but these effects have not been observed consistently in subsequent studies. The effects of betaine on growth-performance parameters, although modest and variable, are most often positive. Interactions between betaine and sex have been consistently observed; however assessment of interactions with other dietary factors (especially methionine, choline and lysine) has been limited and requires additional research before definitive conclusions can be made.

Carnitine

Compared to betaine, far fewer studies have been reported regarding the feeding of carnitine to swine, and similar to betaine, none of the "industry-driven" research has been published in peer-reviewed articles. Numerous studies with neonatal swine (Baltzell et al., 1987; Coffey et al., 1991; Honeyfield and Froseth, 1991; Kempen and Odle, 1993, 1995; Penn et al., 1995) would suggest that newborn piglets may be compromised in their carnitine status. Studies with weaning-aged swine (Weeden et al., 1990; Newton and Burtle, 1992) have reported improvements in growth performance (daily gain and gain/feed) when supplemental carnitine (ranging from 25 to 6000 ppm) was fed, and interactions with dietary fat and lysine have been suggested but not substantiated. More recently, effects on growth performance and carcass composition in growing-finishing swine also have been observed. In a dose-

Table 2. *Effects of betaine (BT) supplementation to swine diets on average daily gain (ADG), feed intake, gain/feed (G/F), carcass backfat (BF) and loin area/depth (Loin): Summary of published abstracts†*

1st Author	No. of Pigs		Sex	Genotype	Other Treatment	Wt.kg	Betaine (BT) Main Effects and Interactions‡				
	Total	Per Trt					ADG	Intake	G/F	BF	Loin
Smith 1994	64	16	M	constant	Cr & carnitine	34-102	NS	NS	NS	NS	NS
Matthews	32	16	G	constant	none	56-109	NS	NS	NS	NS	NS
Cera	288	24	B,G	Hi & Lo Lean	none	83-116	NS	BT-Sex	BT-Sex	NS	NS
Webel	200	25	B,G	crossbred vs PIC	none	83-118	BT-Sex	NS	NS	NS	NS
Smith 1995	80	16	G	constant	choline	61-104	BT	NS	NS	NS	BT
	262	90/172	M	constant						NS	BT
Campbell	88	11	I,G	constant	Met	65-100	NS	NS	BT-Met	NS	
Lawrence	400	50	B,G	constant	Lys	60-110	BT-Lys	NS	NS	BT-Sex	NS
Haydon	80	10	I, G	constant	Lys/cal	71-	NS	BT-Sex	BT-Lys		
	160	20	G	constant	Lys/cal	103-	BT-Lys	BT-Lys		BT	BT
	160	10	B	constant	DE, " "	101-	BT-DE	BT-DE		BT-Lys	BT-Lys

†, Other abbreviations used: B = barrow, G = gilt, M = barrows and gilts mixed, I = intact males, Lys = lysine, Met = methionine, DE = digestible energy, cal = calorie, BT = betaine.

‡, All reported effects ($P < 0.05$) and trends ($P < 0.10$) are included. Betaine main effects are indicated as "BT", interactions are tabulated as "BT-Effect", and non-significance is designated as "NS". Shaded cells signify negative effects of betaine. When data were not collected or reported, cells are blank.

response study (with carnitine fed at 0, 25, 50, 75, 100 or 125 ppm), Owen et al., (1994) reported quadratic responses in loin muscle area and carcass backfat, with 50 ppm carnitine providing the best response. Similar carnitine effects on carcass characteristics were observed by Smith et al. (1994) who also detected improved growth performance (daily gain and gain/feed) during the grower phase. Newton et al. (1994) also reported that carnitine fed at 10 ppm during the finisher phase reduced days to market (105 kg) by 2 days. They also observed that backfat was reduced when increasing carnitine was fed to gilts and light-weight barrows.

Summary and Conclusions

The desire for lean pork among health-conscious consumers has motivated swine nutritionists to develop feeding strategies which maximize lean accretion and limit fat deposition. Recent research suggests that supplementation of swine diets with betaine or carnitine may help to achieve this goal.

Although betaine and carnitine are structurally similar and both can be synthesized by mammalian species, their roles in metabolism are very different. Catabolism of betaine provides methyl-carbon for various biosynthetic reactions, and intact betaine may serve as an osmotprotetant for certain cell types. In contrast, carnitine is not degraded by mammalian enzymes, but serves as a cofactor for the transport of organic acids across biological membranes; most notable being the transport of long-chain fatty acids across the inner mitochondrial membrane for subsequent oxidation.

Many swine-growth studies examining effects of supplemental betaine and carnitine have been conducted under both field conditions and in academic settings, but unfortunately no research has been published in referred journals to date. Among the variety of trials summarized in abstracts, proceedings and field-day reports, several have observed positive (but variable) effects on pig growth performance and (or) carcass characteristics, and some have failed to detect any effects. From the wide variety of experimental designs and the abbreviated reports available, it is difficult to predict conditions under which positive responses will be observed. Therefore, caution must be used in making global generalizations regarding the efficacy of either compound.

In the majority of experiments reported, when statistical effects were detected (on any parameter) they were generally positive/beneficial. Thus it seems prudent for research to continue. However, future work should examine further the mechanisms by which betaine and carnitine may be operating. Additional research should employ methods beyond typical feeding trials and should examine criteria to allow mechanistic hypotheses to be tested. Whether the putative effects of betaine and carnitine are mediated via the established biochemical roles of these compounds or whether they pharmacological in nature remains to be determined.

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VISION OF THE FUTURE

by
STEVEN T. SONKA

Introduction

My charge in this paper and in these brief remarks is to provide one perspective of the future of the Illinois pork industry. To accomplish this difficult task within the time constraints provided, I'll focus on the root causes of change in agriculture within the context of a market economy. It's my hope that by concentrating on these basic forces for change, we'll be able to concentrate on the important implications of change for the future structure of the Illinois pork industry.

The initial segments of the paper will consider general elements of change in business and economic systems. The following section will examine the concept of industrialization of the pork sector in both its business and emotional dimensions. The next section will take an even broader perspective to consider the role of change in market economies. Moving to a narrower lens, the paper's third section will identify and discuss six specific factors affecting agriculture. Because industrialization is inherently a replacement for commodity transactions in agriculture, the next section will contrast the specific factors just noted with the key success factors in a commodity marketing system. The paper's concluding section will consider several implications of this vision, including addressing a question that been asked of me by numerous producers over the last three years--Is the industrialization of pork production inevitable?

What is Industrialization, Anyway?

It's interesting how quickly the phrase, industrialization of agriculture, has become a commonly used and accepted descriptor of the changes occurring in agricultural production and marketing. As is the case for many commonly accepted terms, often each of us has differing perceptions and associations with the term. However, we typically assume that our perception is basically the one being used by everyone else.

Consider, for example, the term quality as we think about the pork sector. In a room of producers, packers and consumers we're likely to find that "pork quality" evokes images that include:

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leanness
taste
uniformity of color
consistency of size
absence of foreign objects (i.e., needles) and
the extent of "moral" practices used in production.

any effective discussion of enhancing pork quality needs to recognize and distinguish among these differing attributes.

Similarly, it's important that we address definitional issues for the term, industrialization of agriculture. In a 1991 article in Choices magazine, Tom Urban provided one such definition:

- The process by which consumers' wants and needs are fed back to production and distribution systems to provide desired quality, availability and price.

This definition is informative because 1) it focuses on consumers, 2) it provides a perspective that extends beyond agricultural production, and 3) it explicitly includes quality as an attribute.

In a 1994 symposium, the Council on Food, Agricultural and Resource Economics provided a similar, but more extensive, definition:

- Industrialization in agriculture refers to the increasing concentration of farms and to vertical coordination (contracting and integration) among the stages of the food and fiber system. The emerging system is expected to be highly competitive in global markets, more efficient, more responsive to consumer demands, less dependent on government assistance, and able to more rapidly adopt new technologies.

This perspective identifies two of the direct impacts of industrialization (larger farms and vertical coordination) and specifies economic and market effects expected.

Examining these two definitions, it's difficult to see how there could be any controversy regarding the desirability of industrialization (except maybe that the word itself evokes images of factories and smokestacks). If industrialization proceeds, however, significant changes in the framework of relationships within the agricultural system will follow. And, although no one may argue with the desirability of better serving consumers, there can be considerable controversy about the changes required to achieve that general goal.

American agriculture, and its predominant family farm structure, evoke strong images and perceptions. These images almost always focus on the agricultural production unit even though, as depicted in Figure 1, there are numerous economic actors between genetic input providers and consumers. In Figure 1 there are dark heavy lines that separate the symbol for production agriculture, the barn, from the other sectors. We use those lines 1) to indicate the existence of

commodity-type, short-term market transactions on each "side" of the farm gate and 2) to illustrate the perception of the independent family farm unit.

From some perspectives, increased industrialization in agriculture attacks that very strong image of the independent family farm. (As is typically done, let's conveniently ignore the major interrelationships between government farm programs and the perceived independence of the family farmer in this discussion.) Using the visual tool of Figure 1, industrialization is in effect rubbing out segments, or all of, those dark lines around the agricultural production unit. And, in doing so, we perceive that some of the desirable features of the idealized independent family farm are threatened.

Market Economies and Creative Destruction

The preceding two definitions are heavily rooted in economic concepts and theories regarding the development of production and marketing systems to serve consumers. Implicitly at least, the concept of consumer sovereignty within a market economy is the cornerstone for these definitions. Before proceeding to examine specific change factors, we need to consider some essential principles that undergird the evolution of market economies.

In the 1930s, two European economists developed theories of how economies worked and changed. One, John Maynard Keynes, focused on the macro economy. Based upon the notion of describing the natural forces that led the economy to equilibrium, Keynesian economics was particularly appropriate for examining the role of large institutions, especially the role of government policy in times of depression. Keynes thinking served to underpin much of the macro economic thinking of the post-War period.

The second economist, an Austrian named Joseph Schumpeter, developed concepts that approached the economy from very different perspectives. Whereas the implicit norm in a Keynesian world is equilibrium, Schumpeterian economics takes disequilibrium as the norm. Here the focus is on natural forces that cause change in the economy. It's intriguing that in the last decade, Schumpeter's work has reemerged as a force in economics.

This reemergence of interest really has its origins in the reality of the marketplace of the late 1980s and 1990s. In this business environment, managers (especially American managers) found that:

- **great** performance today
    - is likely to be only **OK** if repeated tomorrow but
        - is likely to be **not good enough** if repeated the day after tomorrow.

Schumpeter's work explains the manager's treadmill through the concept of Creative Destruction, which he argues is the essential fact about capitalism. Further, Schumpeter asserts that:

Capitalism is by nature a method of economic change...

> ***..coming from new consumer goods,***
> ***..new methods of production,***
> ***..new markets, and***
> ***..new market systems***
>
> ***..revolutionizing the economic structure from within,***
> ***incessantly destroying the old one,***
> ***incessantly creating a new one.***

Schumpeter's powerful words don't relate just to agriculture and agricultural markets. Indeed that is why they are so important for those of us interested in the industrialization of agriculture. These words stress that throughout market economies there will be incessant and continual pressure to industrialize---to improve production and distribution systems so as to better serve consumers.

Six Specific Drivers

The Creative Destruction perspective sets a stage within which specific factors impact upon agriculture and the other sectors of the economy. Now let's examine six specific forces that are distinctly affecting the agricultural industrialization. These are listed in Figure 2 and each will be briefly considered in the following remarks.

Changing Consumers: Especially in the United States, consumers have learned to expect not just good, but continually improving, performance in the marketplace. Indeed, this is the ultimate expression of Creative Destruction. Consumers have come to expect both variety and excellence in the offerings they are provided in the market.

In developed economies especially, the marginal dollar for a food product competes not just with other food products but with all other potential uses of the consumer's dollar. As a result providing large quantities of safe foodstuffs to meet average nutritional needs, although an important societal goal, is not effective in competing for additional consumer dollars. Instead the ability to segment markets, including segments based upon attributes created on the farm, is emerging as a means to compete for agriculture's share of the consumer dollar (Sonka).

Customers and Continual Improvement: For pork, as for most agricultural products, intermediaries, "the evil middleman," stand between the producer and the final consumer. In reality, these food processors and manufacturers are the farmer's customers. As suppliers, food processors have learned that defining quality in terms of customer needs and striving to continually improve are essential to survive and succeed. As customers, food processing firms 1) are developing similar expectations for their suppliers and 2) are increasingly viewing agricultural producers as suppliers (Sonka). Effective customer/supplier relationships have very different characteristics than do adversarial, open market commodity transactions.

Societal Accountability: It is clear that society has become concerned with the practices and procedures employed in producing its foodstuffs. Specific examples relating to the environment, food safety, and labor practices are readily available. Whereas a commodity market operates with information about price and physically measured quality attributes, responding to societal concerns often means that additional information attributes (about the how, where, and when of production) need to be incorporated into the market. As these pressures increase, the commodity market becomes less effective in responding to consumer needs.

Farmers as an Endangered Species: Any casual reading of demographic data for farm operators will tell a powerful story. The average age of farmers is increasing, the proportion of younger farmers is decreasing, and the proportion of agricultural production being conducted by farmers at, or exceeding, typical retirement ages is increasing.

Although not supported by any empirical evidence, it appears to me that the attitudes and expectations of those young people most likely to pursue livelihoods in agricultural production has changed in the last 10 years. Possibly because of the negative experiences associated with the farm financial stress of the 1980s, there seems to be more interest in pursuing a career in production agriculture and less enthusiasm for becoming an "independent family farmer".

These two trends suggest that attracting future management and labor to agriculture may require a differing production structure than that which American agriculture has grown accustomed to.

Technology and Precision Agriculture: Anyone who has paid any attention to the farm media over the last two years couldn't help but be introduced into the information age and its potential impact. There are two key elements here:

- Information technology-based monitors and sensors allow us to consistently, repeatedly and efficiently collect production data. This means that information collection, production processes, and decision making can be done with considerably more precision.
- The Internet and associated electronic communication technologies promise to change the flow of communications within the agricultural production and distribution system. Relative to farm inputs, dialogue between farmers and their suppliers can start to replace mass communication and advertising. On the farm output side, information flows regarding consumer needs can now extend to the farm production level.

Government's Changing Role: For the last 50 years, government farm income support has been a characteristic of commodity agriculture, especially for key crops. Although pork production has not been directly included within income support programs. However, the price stability associated with corn production has had implications for pork production and planning.

Throughout agriculture, an effect of the farm income support programs has been to reduce income variability and provide an assured market for producers of those commodities directly affected by government programs. The presence of this assured market also had the effect to negate incentives for the development of supplier/customer relationships between farm producers

and food processors. As, or if, government income support declines, it is likely that supplier/customer relationships will emerge.

The Strengths of Commodity Agriculture Versus Creative Destruction

In a popular marketing strategy book of the 1980s, Ries and Trout stipulated that one of the keys to successful marketing was to attack the weakness inherent in the market leader's strength. For our purposes we can consider commodity agriculture as the market leader and, in the sense of Competitive Destruction, industrialization is attacking the weakness of commodity agriculture's strength.

Commodity agriculture has been very successful in doing what it was designed to do -- producing and delivering large quantities of undifferentiated output at relatively low cost. We who are involved agriculture should, from a societal perspective, be proud of and celebrate that success. But if we believe in Creative Destruction, we should expect that success to inherently lead to change.

The marvel of commodity agriculture is linked to its efficiency in coordinating a massive, geographically dispersed system at low cost. To accomplish this, the commodity system relies on the features of anonymous transactions, relatively coarse quality standards, and a focus on price and quantity information. These features are strengths in achieving the goals of a commodity system.

These same feature are weaknesses, however, in attempting to respond to the driving forces noted previously. Attempting:

- to more effectively serve niche final consumer needs,
- to develop tighter supplier/customer linkages, and
- to establish information systems to accommodate societal concerns

all run counter to the inherent strengths of commodity agriculture.

An additional feature of commodity agriculture is that improvement tended to come from outside the system, especially outside the farm firm. Because of the historically high cost of data systems within production agriculture, improvements tended to occur in the form of technological improvements emanating from outside the farm firm. Although historically successful, we know from other industries that this approach can be significantly enhanced if decision makers learn from the data created within their own production operations.

Precision agriculture offers that capability. However, precision agriculture can be most effective in creating improvement only when production information is linked with data on performance of the farm output within the customer's operations. Exploiting these improvements requires movement away from a commodity approach and towards industrialization.

Summary thoughts

The preceding remarks have provided one perspective of the future, by focusing on those general forces that affect production systems in a market economy. This perspective should allow each of us to shape a specific vision of the future of the pork industry. Whatever our individual vision, hopefully that vision is enhanced by subjecting it to the rigors of market economics.

In summary, there are three important questions that warrant consideration by those of us particularly concerned with the future of the Illinois pork industry. These are:

- An agricultural system that is truly market driven and customer responsive is likely to employ market linkages and relationships that differ from those of commodity agriculture. Making effective decisions in such a setting will require new skills for farmers. How will those skills be acquired?

- Societal accountability is often viewed as a threat by the agricultural community. Others see an opportunity in providing agricultural products (differentiated by how they are produced) to consumer segments desiring those attributes. In reality, heightened levels of accountability probably represent elements of both opportunity and threat. How can producers effectively respond to society's interest but mitigate the elements of threat and exploit the opportunities?

- Precision agriculture, in conjunction with electronic communication capabilities, offers a historic opportunity for the agricultural system. As massive amounts of production data are captured, analysis and communication of that data will enable the creation of information and knowledge that is not now available. Learning has been shown to be a powerful strategic tool in many industries. How will effective systems to maximize learning be created and employed?

Finally, I want to address the question raised in the paper's introduction -- Is the industrialization of agriculture inevitable? The Schumpeterian view of Creative Destruction helps us answer that question and also should allow us to better frame our discussion of the implications of industrialization in pork production.

> If we adopt the notion that capitalism is by nature a method of economic change, we should see that the issue is **NOT** the inevitability of industrialization in agriculture. The real issue is the inevitability of **consumer choice**.

Remembering that industrialization is driven by the market system's drive to better serve consumers, one implication is clear. The economic health and vitality of agriculture will suffer if industrialization does not occur. One of the purposes of a market economy is to relentlessly punish those economic entities that don't continue to better serve their customers and final consumers. Therefore, as we consider the implications of industrialization of agriculture, let's remember that NOT industrializing has significant implications as well.

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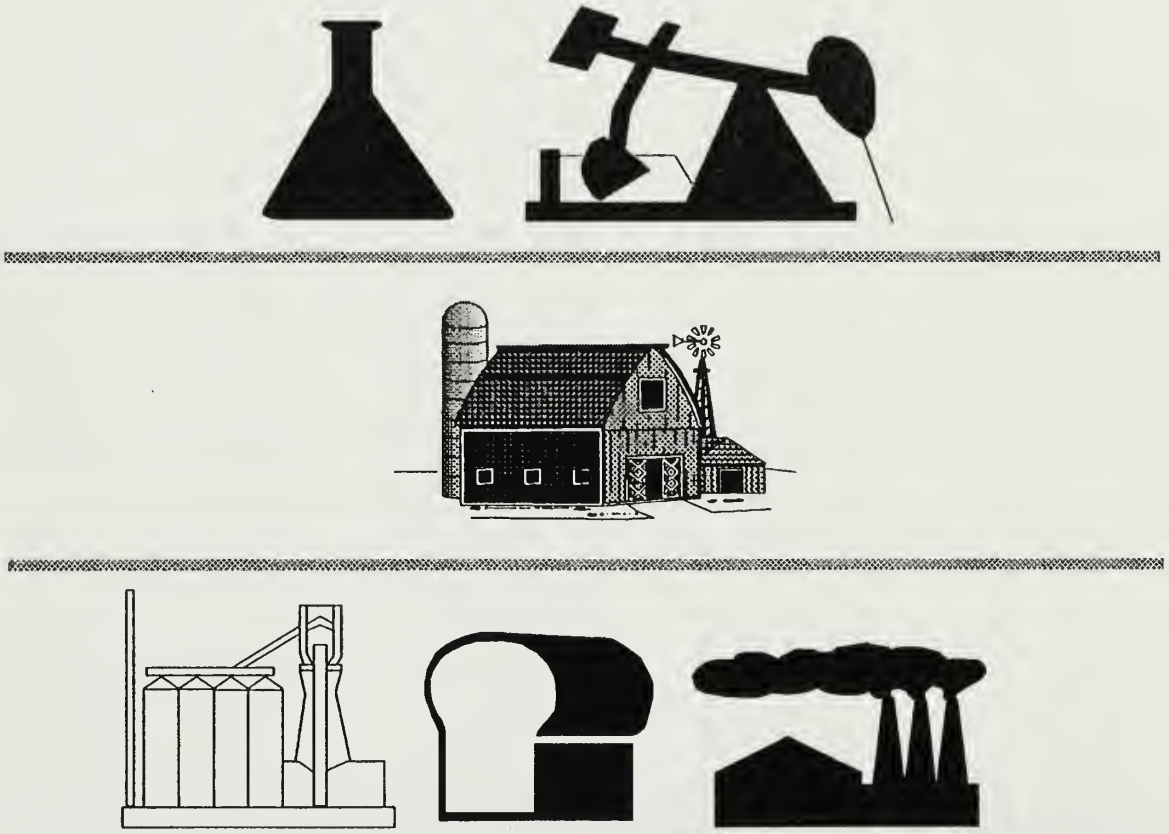

Figure 1

Driving Forces for Change

Changing consumers

Customers and continual improvement

Societal accountability

Farmers as endangered species

Technology and precision agriculture

Changing role of government

Figure 2

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